

A DEMOGRAPHIC ANALYSIS OF LESSER PRAIRIE-CHICKEN POPULATIONS
IN SOUTHWESTERN KANSAS: SURVIVAL, POPULATION VIABILITY, AND
HABITAT USE

by

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ABSTRACT

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat and populations have been reduced range-wide by more than 90% since the turn of 20th Century. Population indices in Kansas reflected the range-wide trends. The rate of habitat loss slowed considerably starting in the 1980s, but populations have continued to decline in the state. To aid in the conservation of this “warranted but precluded” threatened species, more information is needed on the basic and applied population ecology of this prairie grouse. The present research was initiated to collect field data for 3-years and synthesize 6-years of data from 2 Federal Aid projects in southwestern Kansas.

I used age-structured mark-recapture models to estimate the local survival rates of banded yearling and adult male lesser prairie-chickens from live mark-recapture data. Local survival rates of male lesser prairie-chickens were ranked: yearling ($\phi^1 = 0.615$, SE = 0.068) > adult ($\phi^1 = 0.485$, SE = 0.058) > older adults ($\phi^2 = 0.347$, SE = 0.047).

Using joint models of live encounter and dead recovery, I examined the potential for bias in survival estimates of radiomarked male lesser prairie-chickens. The model best supported by the data, $\hat{S}_c, p_{group+t}, r_g, F_c$, indicated that survival was best modeled as not different ($\hat{S}_c = 0.731$, SE = 0.072) across radiomarked and banded birds.

I evaluated the effects of season, age, and gender on survival of radiomarked birds. The known-fate analysis revealed that overall male ($\hat{S} = 0.71$, SE = 0.06) and hen ($\hat{S} = 0.69$, SE = 0.06) survival rates were similar, but hens were most susceptible to mortality during nesting. Additionally, yearling females had a greater probability ($\hat{S} = 0.77$, SE = 0.06) of surviving than adults ($\hat{S} = 0.62$, SE = 0.05).

Population viability and management alternatives were examined using elasticity analysis on an age-specific projection matrix. The model was parameterized with demographic data from this field study. The rate of population change (λ) was < 1.0 for both populations ($\lambda^I = 0.544$, $\lambda^{II} = 0.754$). This indicated a short-term decline in population growth in the absence of immigration. However, the marked contrast in the contributions to λ between populations were explained by nest success and chick survival, and prescribed management practices should focus on these rates.

I examined the relationship of several habitat characteristics and landscape features as they pertained to habitat suitability in southwestern Kansas. I quantified these characteristics in use and non-use sites as determined from the presence or absence of prairie chicken locations. Multivariate analyses indicated that site occupancy was explained, in part, by moderate densities of sagebrush, but negatively associated with the proximity to anthropogenic features (e.g., powerlines, roads, buildings, and pump-jacks).

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INTRODUCTION

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is one of 3 prairie grouse in the genus *Tympanuchus*. Similar to its congeners, the greater prairie-chicken (*T. cupido*) and sharp-tailed grouse (*T. phasianellus*), the lesser prairie-chicken requires native grasslands or shrublands for breeding, nesting, brood rearing and survival, but has one of the most restricted ranges of North American grouse (Giesen 1998). The lesser prairie-chicken occupies mixed-grass and shrub prairies in Colorado, Kansas, New Mexico, Oklahoma, and Texas. The sand sagebrush (*Artemisia filifolia*) prairies consisting of bluestem (*Agropogon* spp.) and dropseed grasses (*Sporobolus* spp.) occur in the sand hills of Colorado, Kansas (south of the Arkansas River), the northeastern panhandle of Texas, and Oklahoma. The sand shinnery oak (*Quercus havardii*) savannas occur in southeastern New Mexico, and the southwestern panhandle of Texas. The mixed-grass prairie with little or no shrub component occurs north of the Arkansas River in Kansas.

Although lesser prairie-chicken range was limited historically, human disturbances have further reduced its distribution and abundance (Giesen 1998, Woodward et al. 2001, Fuhlendorf et al. 2002). The continued destruction and degradation of the mixed-grass prairies has been the primary cause of the population declines since the turn of the 20th century (Taylor and Guthery 1980). It is hypothesized that lesser prairie-chicken habitat has sustained a loss of >97% and population abundance and distribution paralleled those losses (Taylor and Guthery 1980). Much of the early habitat loss was attributed to extensive dry-land agriculture throughout the mixed-grass prairies, followed by the Dust Bowl of the 1930s. During the 1960s the development of

center-pivot irrigation systems revolutionized agriculture in the semi-arid regions of the southern Great Plains. This initiated a second wave of habitat loss and fragmentation that lasted until the 1980s (Waddell and Hanzlick 1978). Although such large-scale conversions of lesser prairie-chicken habitat have slowed, insidious changes to the landscape have taken their toll (Woodward et al. 2001). Urbanization and suburban housing developments, energy development, and invasion of woody species such as eastern red cedar (*Juniperus virginiana*), osage orange (*Maclura pomifera*), and mesquite (*Prosopis* spp.), are all sources of habitat loss or degradation.

Despite the general slowing trend in habitat loss, lesser prairie-chicken populations have continued to decline range-wide (Braun 2000). Given its restricted range, and isolated and unstable populations, the lesser prairie-chicken was petitioned for listing as threatened under the Endangered Species Act in 1995 (U.S. Fish Wildlife Service 2002). The U.S. Fish and Wildlife Service (USFWS) determined that such a classification was “warranted but precluded” due to other species priorities. Currently the priority for listing the lesser prairie-chicken is reviewed annually by the USFWS.

The conservation concern for the lesser prairie-chicken has warranted a substantial body of both applied and basic research. In this introduction, I will outline historical distribution and abundance of lesser prairie-chickens in Kansas, provide insight to some of the knowledge gaps for the species, and indicate how I addressed those in the following chapters of my dissertation.

LESSERS PRAIRIE CHICKENS IN KANSAS

Past distribution

The first studies of lesser prairie-chickens in Kansas (Baker 1953, Schwilling 1955) documented the species in 14 counties throughout sand sagebrush prairies, generally south of the Arkansas River (Fig. 1). Baker (1953) confirmed a record of a lesser prairie-chicken taken in January 1921 from Logan County in the northwestern portion of the range (Fig. 1). Baker (1953) also noted a correspondence with a state game protector (SGP) of Kansas Department of Wildlife Parks (KDWP) indicating that lesser prairie-chickens once occupied counties as far north as Ellis, Ness, and Graham. Schwilling (1955) documented 2 relatively small populations of birds at the periphery of the known range in 1955: 1) on the border of Scott, Lane and Finney counties, and 2) along the border of Finney and Hodgeman counties (Fig. 1). White (1963) reported prairie chickens of unknown species in Ness and Hodgeman counties (Fig. 1). Waddell (1977) summarized rural mail carrier survey observations of prairie chickens from 1962 to 1976, and found prairie chickens (species not identified) as far north as Ellis and Russell counties. Observations in eastern counties included: Ellsworth, Rice, Reno, and Harper (Fig. 1). Horak (1985) surveyed district biologists and SGPs to identify the distribution of both prairie chicken species in 1980. Notably biologists and SGPs from Region 6 (i.e., mixed prairies north of the Arkansas River) indicated the presence of 10% lesser prairie-chickens, 10% unknown species, and 80% greater prairie-chickens (Horak 1985). Region 1 (the core of the lesser prairie-chicken range) was reported as having 5% unknown species apparently in Hodgeman County. While inconclusive, these reports combined suggest that the lesser prairie-chicken has occupied various habitats throughout

the western portion of the state over the last 100 years. If this distribution has fluctuated naturally through time, it is likely dependent upon changes in the moisture gradient and changes in land use (Baker 1953).

Present distribution

Currently lesser prairie-chickens occupy much of the range described above although the abundances have declined (Fig. 1). In 1997, it was reported that substantial numbers of lesser prairie-chickens were documented north of the Arkansas River in northeastern Finney and western Hodgeman counties (KDWP unpublished data). As the effort increased to document lesser prairie-chickens north of the Arkansas River more populations were identified (KDWP unpublished data). Notably 4 counties have first reported records of lesser prairie-chickens, Gove, Greeley, Wallace, and Wichita (Fig. 1). Currently lesser prairie-chickens have been documented from listening surveys in 16 counties north of the Arkansas River. Although 10 established KDWP survey routes south of the Arkansas River have indicated long-term declines, it is less clear as to the long-term trends in the northern portion of the state. Lesser prairie-chickens currently occupy 31 of 39 counties estimated to have been occupied historically (Jensen et al. 2000).

Abundance

Lek survey data (1964 -2002) from 10 survey routes indicated that over the long-term, population indices have declined (Fig. 2). Jensen et al. (2000) quantified this relationship through 1999 and indicated that year explained little of the variation in the data, but the declining slopes were significantly different from zero. I examined the relationship between lek survey data (number of birds/mi²) qualitatively and the amount

of pastureland available in each county where survey routes occurred. As an index to available rangeland for prairie chickens I used U.S. Census of Agriculture data (1964-1997) on acreage of pastureland. These data were collected at approximately 5-year intervals; thus I averaged lek count data as bird/mi² for the interval between censuses. I used English units of measure to maintain consistency with KDWP databases. I assumed that land use had not changed since 1997 and used the same pastureland values for 2002. The resulting plot (Fig. 2) indicated a threshold effect where prairie chicken indices increased as some portion of land was converted to agriculture but crashed in the early 1980s. Although the amount of pastureland in these survey routes has changed little in the past 20 years, populations have continued to decline. Jamison (2000) found a significant non-linear relationship for the Finney County survey data as it related to the number of irrigation well permits issued in a given year. Thus, both of these independent measures of land use suggest potential long-term negative impacts of large-scale conversions of native rangeland to agricultural land.

KNOWLEDGE GAPS

The “warranted but precluded” status listing of the lesser prairie-chicken has initiated a significant amount of research examining both intrinsic as well as extrinsic factors that may be contributing to population trends. Surveys of disease (Hagen et al. 2001, Peterson et al. 2002, Wiedenfeld et al. 2002), helminthic parasites (Robel et al. in press), and genetics (Van den Bussche et al. 2002), generally, have reported that these intrinsic factors were not limiting the populations. Alternatively, Woodward et al. (2001) identified landscape characteristics that were correlated with declining and stable populations. Generally, populations occupying landscapes with slow rates of shrubland

habitat loss, were more stable than populations in landscapes with faster rates of habitat loss. Most of this shrubland loss had been to either woody encroachment or suburban development (Woodward et al. 2001). However, these changes in landscape were not linked with demographic rates. Jamison (2000) suggested that depressed demographic rates such as nest success and chick survival were the primary limiting factors in southwestern Kansas. Jamison (2000) also examined survival rates and probable causes of mortality of radiomarked males and females for 6-month periods (Apr-Sep). From Jamison's (2000) work it was suggested that adult survivorship during summer and early fall was not a limiting factor. Winter survival was estimated for 1 year for males and suggested that it was not less than that of summer.

Few data exist on the demography of the lesser prairie-chicken. Although short-term studies (≤ 3 years) have quantified nest success (Riley et al. 1992, Giesen 1994) and annual survival (Jamison 2000), only 1 study (Campbell 1972) estimated survival from 10 years of band recoveries. No studies have taken a comprehensive approach to analyzing the demography and life-history strategy of the lesser prairie-chicken.

Evaluating age-specific variation in survival has been a central tenet of avian population biology (Martin 1996). Such information is necessary for understanding population dynamics and life-history strategy. Age-specific susceptibility to predation and harvest has been of particular interest to researchers working on species of conservation concern. The timing of mortality and annual survival are important demographic rates in the study of life history, mating systems, and management actions (Caizergues and Ellison 1997). Understanding the annual variation in the timing of mortality and its severity are especially important for grouse species management

(Bergerud 1988), as females in promiscuous mating systems (unipaternal care) may have an increased mortality risk during incubation and brood-rearing periods. Age-specific survival has not been previously examined in the lesser prairie-chicken, and may yield important insights to population dynamics.

Age-specific survival and fecundity are important vital rates as inputs to population viability and sensitivity models. Previous demographic modeling of greater and Attwater's prairie-chicken (*T. c. attwateri*) indicated that nesting, chick survival, and post-brood survival (i.e., survival from fledging to first breeding) had the highest elasticities, and would be predicted to have the greatest effect on population growth (Wisdom and Mills 1997, Peterson et al. 1998). This coincides with Bergerud's (1988) assessment of all grouse species that recruitment is the driving force behind population cycling and persistence. Despite the tenuous status of the lesser prairie-chicken, no comprehensive demographic analyses have been conducted, because annual and/or long-term data sets are limited on this species.

Lesser prairie-chicken habitat use has been examined at the landscape (Jamison 2000, Woodward et al. 2001, Fuhlendorf et al. 2002), and microhabitat scale (i.e., vegetation characteristics at nests or use sites). While both types of studies have demonstrated prairie chicken affinity for vegetation classes and structure, none have examined habitat use as it pertains to human structures within a given landscape (i.e., meso-scale use). Understanding what features within a habitat patch make it less suitable is critical to future assessment and conservation planning for lesser prairie-chickens.

The primary objective of my dissertation was to synthesize and examine the sensitivity of lesser prairie-chicken demography to changes in various vital rates. Vital rates identified as having the largest impact on population growth rates should be priorities for conservation efforts (Caswell 2001). I compared the demography of 2 lesser prairie-chicken populations in southwestern Kansas.

This study is the culmination of 2 Federal Aid in Wildlife Restoration projects, W-47-R and W-53-R. Field work for W-47-R began in spring 1997 and was completed in November 1999, and W-53-R was initiated in December 1999 and concluded in March 2003. The objectives of this research were to 1) examine the age-specific survival rates of male lesser prairie-chickens from mark-recapture data, 2) examine the potential biases in survival estimates of radiomarked males, 3) examine known-fate survival rates for 9-month period (1997-2002) and the timing of mortality for males and females, 4) examine known-fate survival rates for a 12-month period (2000-2003) and timing of mortality for males and females, 5) identify the probable cause of mortality in radiomarked birds, 6) determine the stability of population growth using Leslie matrix models, 7) identify vital rates to which population growth rate was most sensitive, and 8) model the probability of within patch habitat use based on anthropogenic features on the landscape. This dissertation is presented in 5 self-contained chapters written in the style of the Journal of Wildlife Management.

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Fig. 1. Historic and current distribution of lesser prairie-chickens in Kansas. Note extra-limital records for several studies denoted by small symbols (see map legend for details).

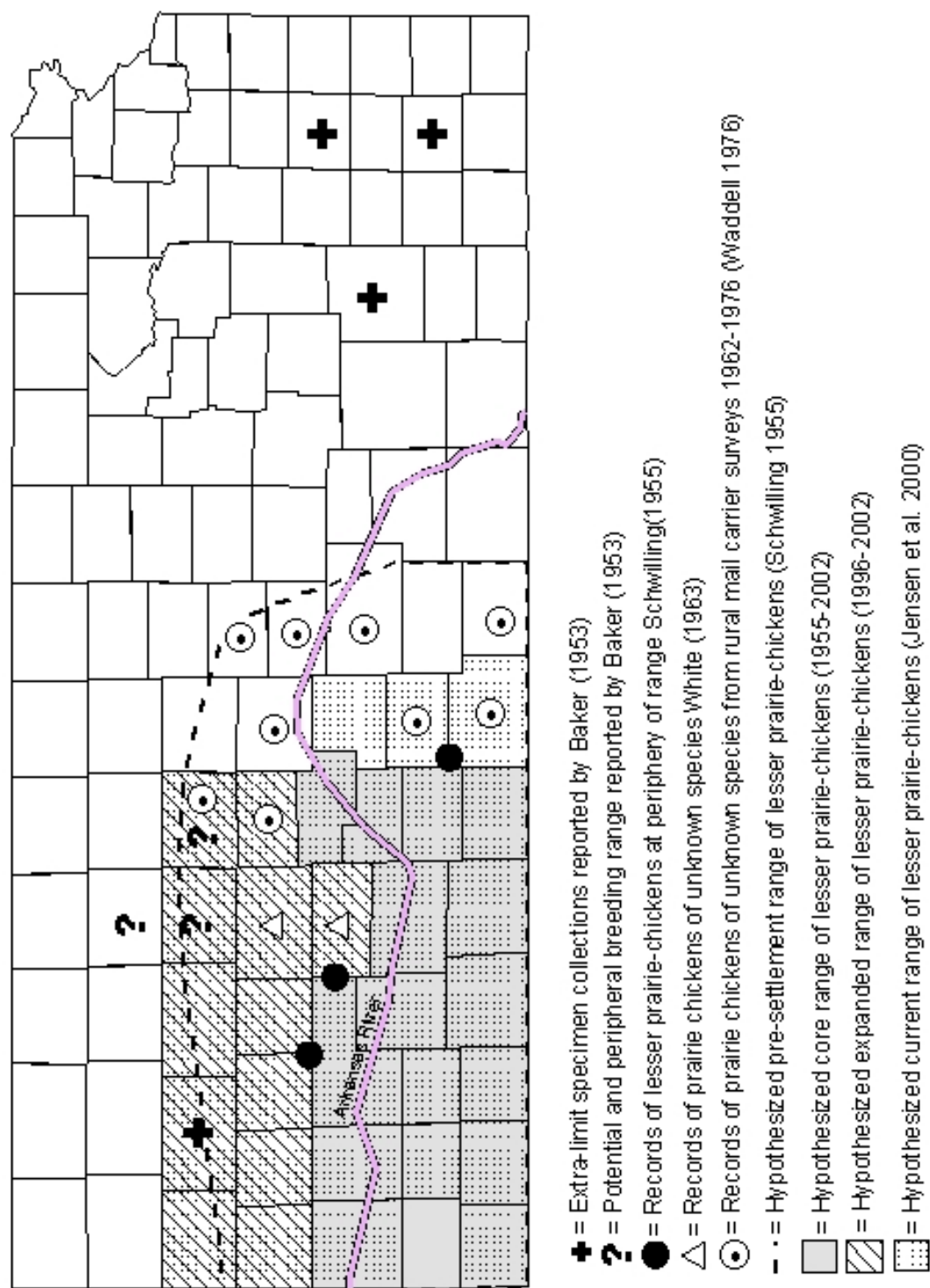
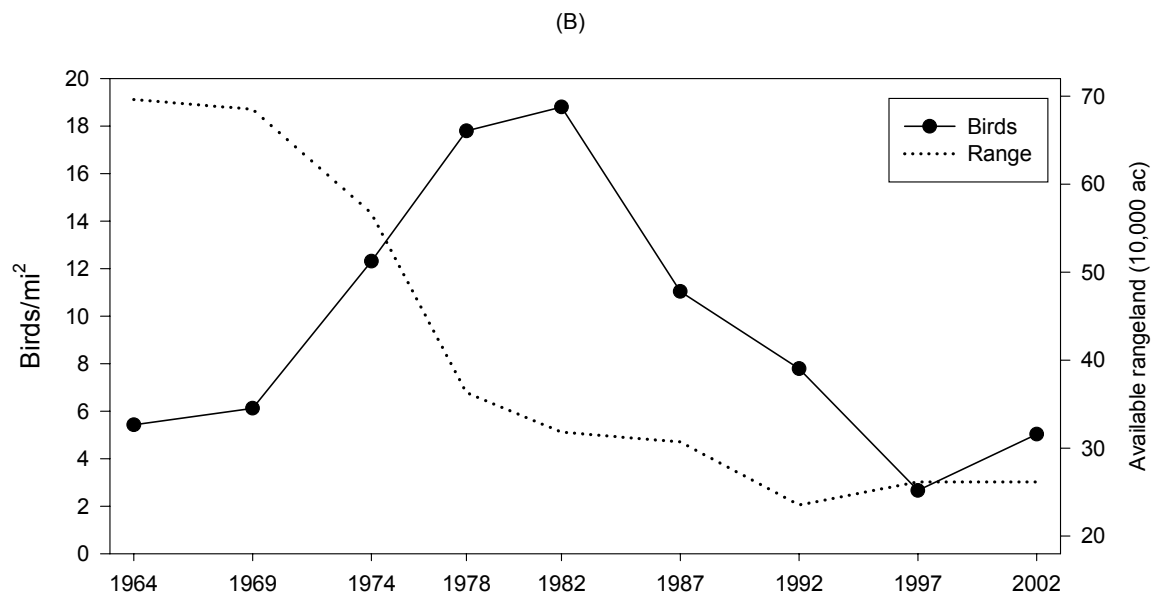
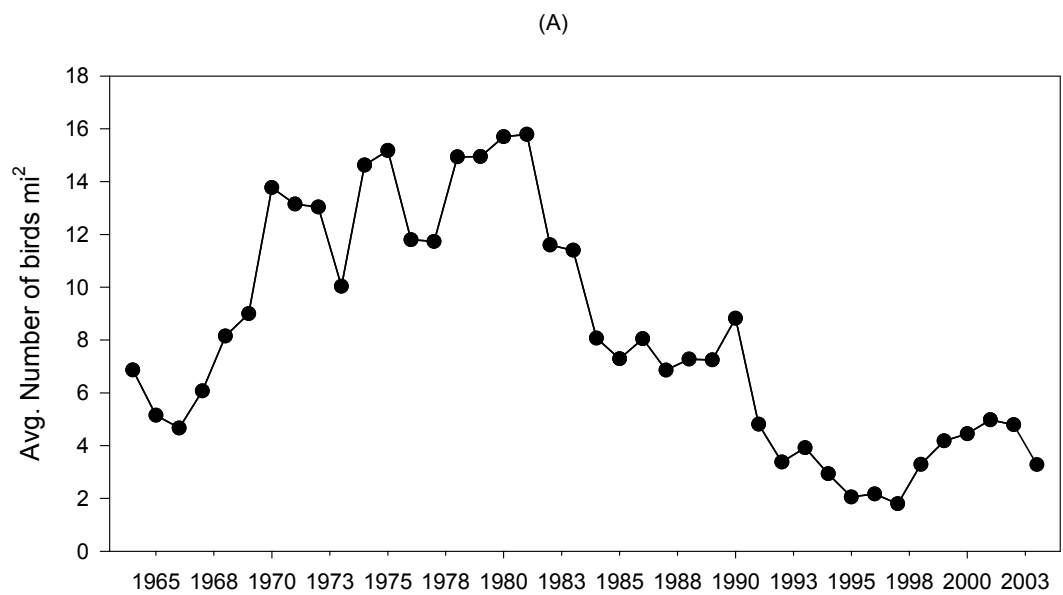


Fig. 2. Population trends (birds/mi²) of lesser prairie-chickens from lek survey data (1964-2002) from 4 to 10 survey routes (A). The relationship between lek survey data and available rangeland for counties where surveys were conducted (B). Five-year intervals were used because U.S. Census of Agriculture quantified available pasture at those approximate intervals. Lek survey data were averaged across each 5-year interval to illustrate the potential long term effects of large-scale habitat loss.



CHAPTER 1

AGE-SPECIFIC SURVIVAL IN MALE LESSER PRAIRIE-CHICKENS

Abstract: Lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat and populations have been reduced by more than 90% since the turn of the 20th Century. To aid in the conservation of this “warranted but precluded” threatened species, more information is needed on its basic ecology. Few data exist on the demography of the lesser prairie-chicken. Evaluating age-specific variation in survival has been a central tenet of avian population biology. I examined the hypothesis of delayed reproductive effort and increased survival of the yearlings in the lesser prairie-chicken. I used age-structured mark-recapture models to estimate the local survival rates of banded yearling and adult male lesser prairie-chickens from mark-recapture data, and used inter-lek movements as an index of site fidelity in southwestern Kansas. I compared these survival rates to other grouse species and mating systems of the holarctic region. I modeled age-structured local survival (ϕ) and recapture (p) probabilities using extensions of the Cormack-Jolly-Seber approach for open populations. Three hundred and seventy-six male prairie-chickens (173 yearlings, 203 adults) were captured from 1998-2002. Local survival rates of male lesser prairie-chickens were ranked: yearling ($\phi^1 = 0.615$, SE = 0.068) > adult ($\phi^1 = 0.485$, SE = 0.058) > older adults ($\phi^2 = 0.347$, SE = 0.047). Twenty percent of recaptured yearlings ($n = 60$) switched leks in their second year, and their odds of switching were 2.5 times as high as those adults (8%, $n = 65$). Lesser prairie-chickens in southwestern Kansas fit models of bimaturism in survival and breeding effort.

INTRODUCTION

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat and populations have been reduced by more than 90% since the turn of the 20th Century (Giesen 1998). To aid in the conservation of this “warranted but precluded” threatened species (US Department of Interior, Fish and Wildlife Service 2002), more information is needed on the basic ecology of this prairie grouse. Few data exist on the demography of the lesser prairie-chicken. Although, short-term studies (≤ 3 years) have quantified nest success (Riley et al. 1992, Giesen 1994) and annual survival (Jamison 2000), only 1 previous study (Campbell 1972) estimated survival from 10 years of band recoveries. No studies to date have examined age-specific rates in survival.

Robust estimates of annual survival are useful for 2 reasons: understanding management efforts and basic science. Survival is one of several demographic rates that can affect fluctuations in population numbers of grouse (Bergerud 1988, Martin 1996). Additionally, age-specific survival and reproductive rates may covary with the type of mating system in grouse (Wiley 1974). Wiley (1974) hypothesized that the evolution of promiscuous mating systems in grouse was a result of 4 concomitant factors: sexual differences in the age at first breeding, sexual size dimorphism, a lack of a need for biparental care for precocial young, and delayed age of first reproduction in males. Foregoing reproduction in yearling males is a trade-off for increased survival in the short-term. This suggests that there is a cost associated with reproductive effort in the promiscuous mating systems of grouse. If true, the predicted pattern in survival for males in promiscuous systems should exhibit a senescent pattern after the first year of reproduction. This pattern may be particularly acute for lek mating species where male-

male competition is more intensive than other promiscuous systems (Bergerud 1988). (A lek is defined as an arena used primarily for breeding, and other aspects of reproduction and life requirements are independent of the lek). Alternatively, yearling males should reproduce in monogamous systems, as there is a lower risk associated with reproductive activity (Wiley 1974).

Few studies have directly examined age-specific variation in life history traits of male grouse (Wittenberger 1978, Lewis and Zwickel 1982). Some studies have indirectly examined these patterns by estimating annual survival of prairie grouse (Robel et al. 1972, Hamerstrom and Hamerstrom 1973, Burger et al. 1991, Schroeder 1997, Giesen 1999). Studies of other promiscuous grouse species have demonstrated age-specific survival rates of males with yearling males surviving better than older birds (Braun 1979, Lewis and Zwickel 1982, Angelstam 1984, Lewis and Jamieson 1987, Zablan et al. 2003). It has been suggested (Wiley 1974, Lewis and Zwickel 1982) that this aging pattern of adult survival is a result of young males foregoing reproduction in the first year and increasing their survival from a lack of reproductive effort (Emmons and Braun 1984).

Most studies on grouse survival have used return rates (i.e., the proportion of marked individuals that are recaptured or resighted in a subsequent year) as an estimate of survival. Interpretation of these estimates can be difficult because return rates are the product of 4 probabilities: true survival (S), site fidelity (F), site propensity (γ^*), and detection (p^*). Alternatively mark-recapture methods of live encounter data can yield improved survival estimates based on return rates by estimating a local survival rate ($\phi = S \times F$) corrected for the probability of recapture ($p = p^*\gamma^*$). Thus mark-recapture

statistics alone cannot estimate true survival, and ancillary data on F are needed to identify potential biases in ϕ .

I examined Wiley's (1974) hypothesis of delayed reproductive effort and increased survival of yearlings in the lesser prairie-chicken. I used age-structured mark-recapture models to estimate local survival rates of banded yearling and adult male lesser prairie-chickens from mark-recapture data, and used inter-lek movements as an index to site fidelity in southwestern Kansas. I compared these survival rates to other grouse species and mating systems of the holarctic region.

METHODS

Study species

The lesser prairie-chicken has one of the most restricted ranges of North American grouse (Giesen 1998), occupying mixed-grass and shrub prairies in Colorado, Kansas, New Mexico, Oklahoma, and Texas. Although lesser prairie-chicken range was limited historically, human disturbances have further reduced its distribution and abundance (Giesen 1998, Woodward et al. 2001, Fuhlendorf et al. 2002). The continued destruction and degradation of the mixed-grass prairies has been the primary cause of the population declines since the turn of the 1900's (Crawford 1974). Conversion of sand sagebrush (*Artemisia filifolia*) habitat to intensive center-pivot agriculture in Kansas ceased in the 1980's, but lesser prairie-chicken populations have continued to decline (Jamison 2000, Jensen et al. 2000). Thus, an examination of the demography of this species is needed to clarify what may be causing the populations to decline in southwestern Kansas.

Study areas

The study region was comprised of 2 fragments (~5000 ha each) of native sand sagebrush (hereafter sandsage) prairie near Garden City, Finney County, Kansas (37° 52' N, 100° 59' W). Work was initiated on 1 area in 1998, and trapping and monitoring efforts were expanded to include the second area in 2000. Prior to 1970, these 2 areas were part of 1 contiguous track of native sandsage prairie. The development of center pivot irrigation left these areas as 2 fragments with about 15 km of agricultural fields between them (Waddell and Hanzlick 1978).

Capture and handling

Lesser prairie-chickens were captured during spring at 20 lek sites using walk-in funnel traps (Haukos et al. 1991, Schroeder and Braun 1991). Traps were placed on all known leks (> 3 displaying males) found in native prairie on the study sites. No attempt was made to trap birds displaying on agricultural fields because these lek sites were unstable. Traps were rotated among groups of 2–3 leks every 7–11 days (trap period \bar{x} = 7.9, SD = 1.7), and each rotation was defined as a trap period. From 1998 to 1999, 2–3 leks were trapped simultaneously on each study area per trap period (3 or 4 periods per spring), and in the 2000 to 2002 portion of the study, 4–6 leks were trapped per trap period (Table 1). At first capture, birds were aged as yearling (~10 months of age) or adult (\geq 22 months) based on shape, wear, and coloration of the ninth and tenth primaries (Amman 1944, Copelin 1963). Yearlings were identified as birds with pointed and frayed tips of the ninth and tenth primaries, and white spotting within 2.5 cm of the tip of the tenth primary. Body mass was measured (\pm 2.5 grams) using a Pesola spring scale. Birds were marked with serially numbered aluminum leg bands. Recoveries of banded

birds were few ($n = 21$) and precluded the use of joint live-encounter dead-recovery models for estimating age-specific survival rates. Ancillary movement data were used from radiomarked birds on the study areas (Jamison 2000, Hagen unpublished data) to examine the potential effects of permanent emigration.

Survival analyses

I modeled age-structured local survival (ϕ) and recapture (p) probabilities using extensions of the Cormack-Jolly-Seber approach for open populations, and following the general procedures of Burnham and Anderson (1998). Mark-recapture analyses were conducted in program MARK 3.0 (White and Burnham 1999) following general steps: 1) selection of the global model, 2) goodness-of-fit tests (GOF), and 3) fitting and selection of reduced models with fewer parameters. Subscripts following parameters indicate explanatory variables (e.g., $\phi_{\text{age} \times t}$ describes a model that includes both age- [yearling or adult as a group effect] and time-dependence in survival). Parameter superscripts “1” and “2” denote the interval after initial release or all subsequent intervals, respectively (e.g., $\phi^1_{\text{age} \times t}$, ϕ^2_t describes a model that features both age- and time-dependence in survival after the initial release, and time-dependence in survival at all subsequent encounters). Lastly, I use a subscript (c) to describe models with parameters held constant (e.g., ϕ_c , describes a model where local survival is held constant).

Global models included age and annual conditions because these factors affect local survival in many other birds (Saether 1990, Martin 1996). Age at first capture was treated as a group effect (e.g., group 1 = yearling, group 2 = adult). I modeled local survival with a modified 2-age class model that separated the interval after first capture (ϕ^1) from all subsequent transitions (ϕ^2). Thus the structure of my global model $\phi^1_{\text{age} \times t}$,

ϕ^2_t, p_t allowed me to evaluate the effects of age on survival after the first capture (Sandercock and Jamarillo 2002). All models were constructed the using design matrices feature and the logit link function in program MARK 3.0.

Bootstrap GOF testing was used to test the 2 assumptions of equal capture and survival probabilities. Model fit was calculated as the rank of the observed deviance from the global model ($\phi^1_{age*t}, \phi^2_t, p_t$) relative to the bootstrap distribution ($n = 1,000$) of model deviance (Cooch and White 2001). If the observed deviance value was $> 95\%$ of the bootstrap data then the model fit was suspect, variances were adjusted for overdispersion, and model selection was based on quasi-likelihood AIC_c ($QAIC_c$)(Andersen et al. 1994). I used bootstrapped estimates of model deviance to estimate the quasi-likelihood parameter or variance inflation factor (\hat{c}) and adjusted the standard errors of parameter estimates (Cooch and White 2001). I calculated \hat{c} as the observed deviance of the global model divided by the mean expected deviance from a parametric bootstrapping (Cooch and White 2001). If \hat{c} was < 1 , then \hat{c} was set to 1.

After examining the fit of the most general models and adjustments for overdispersion were made, models with fewer parameters were fit to the data. I selected the best-fit model based on the minimization of Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and/or \hat{c} ($QAIC_c$) (Burnham and Anderson 1998). Models with differences of AIC_c (ΔAIC_c) values ≤ 2 from the best fit model were considered equally parsimonious. The ratio of Akaike weights (w_i / w_j) between 2 models was used to quantify the relative degree that a pair of models was supported by the data (Burnham and Anderson 1998).

The number of potential models was large, therefore I used a hierarchical procedure to guide model fitting (Lebreton et al. 1992). Because my primary interest was local survival (ϕ), recapture rate (p) was modeled first as a nuisance parameter. Local survival was then modeled in 2 steps. First, the probabilities of local survival at later transitions (ϕ^2) were modeled followed by survival of the first interval (ϕ^1) for the modified-age model (Sandercock and Jamarillo 2002). Probabilities p and ϕ^2 were modeled either with time-dependence (t) or as a constant (c). Age and the age*time interaction from these probabilities were excluded because I assumed that birds first marked as yearlings would have similar survival and recapture rates as adults if they returned after the first interval.

Parameter estimates were calculated from the best-fit model; where there was more than 1 parsimonious model (ΔAIC_c or $\Delta QAIC_c < 2$), I used the model averaging procedure in MARK. The model averaging procedure calculates a weighted average parameter estimates for each transition from all models in the candidate set, weighting estimates by using the Akaike weights (w_i) specific to each model. I did not use the variance components procedure due to the relatively short period of the study, thus overall estimates of standard errors include both process and sampling variance.

Estimation of interlek movements

Local survival is a product of true survival and site fidelity. I aided my interpretation of estimates using knowledge of site fidelity. Natal dispersal of yearling male prairie chickens likely occurs in autumn (prior to my capture intervals), and dispersal movement distances of males are usually localized (Bowman and Robel 1977, Jamison 2000, Pitman 2003). Thus, the frequency of movements of banded yearling and

adult males were examined both within and between seasons to evaluate an overall relationship between survivorship and fidelity. Previous work on other lek-mating grouse has shown a greater frequency of movement between leks indicated a non-territorial male, that was sampling leks for opportunities to reproduce in the future (Wiley 1974, Emmons and Braun 1984). If on the first encounter in a successive year a bird was recaptured on a lek other than the lek of first capture it was defined as a between-year movement. If within a trapping season, a bird was recaptured on a lek other than first capture only during the second encounter it was considered a within-year movement. I use this conservative definition, because it is possible with a greater number of handleings birds may have moved to avoid being handled in the future. A likelihood ratio test was used to examine the propensity of yearlings to move between leks relative to that of adults.

RESULTS

Three hundred and seventy-six male prairie-chickens (173 yearlings, 203 adults) were captured from 1998–2002, and 150 males (78 yearlings, 72 adults) were recaptured at least once (Table 1). Forty-six birds were treated as not released at last capture due to known mortalities of radiomarked birds, removals for a parasite study, permanent emigration, and trap mortalities.

Survival analyses

The parametric bootstrap GOF test indicated that the global model ($\phi^1_{age*t}, \phi^2_t, p_t$) ($P = 0.724$) met the assumptions of mark-recapture analysis, and I did not need to adjust for overdispersion because $\hat{c} < 1$. Thus, I used AIC_c for model selection. Modeling of the recapture probabilities indicated that models with time-dependent and constant

recapture rates were equally parsimonious. Given that I had only 5 capture occasions, capture effort per lek was similar in all years (Table 1), and model selection was identical with p_t but with one less estimable survival rate, all subsequent models were fit with p_c . Model selection based on AIC_c indicated that the most parsimonious model ($\phi^1_{age+t}, \phi^2_c, p_c$) with respect to survival was that which recognized differential survival in the age-classes with an additive time effect (Table 2). Local survival rates of male lesser prairie-chickens were ranked: yearling ($\phi^1 = 0.615$, $SE = 0.068$) > adult ($\phi^1 = 0.485$, $SE = 0.058$) > older adults ($\phi^2 = 0.347$, $SE = 0.047$). Models with annual variation in survival of older birds were not well supported by the data ($\Delta AIC_c > 7$), suggesting that survival at later intervals is best understood as a constant rate.

Interlek movements

Twenty percent of recaptured yearlings ($n = 60$) switched leks in their second year. Their odds of switching were 2.5 times as high ($G = 4.735$, $df = 1$, $P = 0.030$; Table 4) as adults' odds (8%, $n = 65$). Each age-class was approximately equally likely (~17.5 %) to move between leks within a breeding season ($G = 0.035$, $df = 1$, $P = 0.851$; Table 4). However, 4 and 15 % of yearlings and adults were recaptured > 3 times, respectively (Table 4). This suggests that adults had a greater propensity to attend leks (and presumably try to obtain copulations) than yearlings.

DISCUSSION

The major findings of this study were: 1) lesser prairie-chicken males had greater survival in the first transition (yearlings > adults > older adults) than in later years, 2) fidelity to lek sites was higher for adults than for yearlings, and 3) these patterns were unlike most all other birds.

Survival models with additive annual variation in the yearling and adult age classes were well supported by the data. This indicated that yearlings and younger adult males (ϕ^1) were susceptible to similar environmental factors, but older males (ϕ^2) had a consistently lower survival rate. However, this may have been tempered by the relatively short period of my study, and a longer term may have yielded better resolution at these intervals. Although Brown (1978) did not measure survival directly, he indicated that harvest levels and yearling adult ratios of lesser prairie-chickens were positively correlated with the previous year's precipitation. Given the relatively short period of my study, it is difficult to quantify what factors may have contributed to this annual variation in survival.

Local survival (ϕ) has 2 components, true survival (S) and site fidelity (F). If age-specific variation in ϕ was due to F , then permanent emigration should be greater in adults. In fact, the interlek movement data demonstrate the opposite pattern, greater movements among yearlings than adults. Therefore variation in ϕ is likely due to S , and the observed patterns could be even more pronounced, because ϕ is more likely to be an underestimate of S for yearlings.

Radiotelemetry data also indicated low rates of emigration, as only 1 yearling and 1 adult of 119 (1.7%) radiomarked males in this study were known to permanently emigrate during the breeding season. Although, yearlings were more likely to switch leks locally than adults were. The relatively high recapture rates ($p = 0.73$) in this study appear not to have been biased by temporary emigration, as only 1 radiomarked adult male was documented moving between my 2 study sites during the breeding season. Two other males (1 yearling and 1 adult) moved between study sites after the breeding

season. The adult was recovered dead on the area to which he emigrated. The yearling's transmitter fell off several months after he emigrated but he was recaptured at his original lek of capture the following spring.

Survival in grouse

My overall estimates of lesser prairie-chicken survival were slightly elevated when compared to that of other banding studies of prairie grouse (Table 5). Given the various methods used to estimate survival it is difficult to compare these rates directly. I assumed that survival estimates based on return rates were biased low because recapture probabilities were not estimated (Campbell 1972). The range of my estimates (0.234 – 0.792) encompassed most of those reported elsewhere (Table 5), and I conclude that annual local survival of male lesser prairie-chickens is comparable to its congeners.

Evidence for differential survival of yearlings and adults is anecdotal in previous work on prairie grouse (Campbell 1972, Hamerstrom and Hamerstrom 1973) (Table 6). Life-table analyses of greater prairie-chickens (*Tympanuchus cupido*) in Wisconsin were suggestive of age-specific survival (yearling = 0.50, adult = 0.48) but differences in survival rates were < 5% (Hamerstrom and Hamerstrom 1973). Campbell's (1972) data from New Mexico indicated differential survival in male lesser prairie-chickens (yearling = 0.35, adult = 0.30). Thus, age-specific patterns in survival exist but they have not been examined with rigorous quantitative techniques. Wiley (1974) hypothesized that promiscuity in grouse resulted from such age-specific patterns, because yearling male grouse would forego reproduction in their first year, thereby enhancing their probability of survival in the short-term. This prediction assumes a cost of reproduction. The

evidence for such costs would be supported by senescent age-patterns in males, and should occur in other promiscuous grouse species.

These age-specific patterns in survival comes from the most sexually dimorphic grouse species, the blue grouse (*Dendragapus obscurus*), sage-grouse (*Centrocercus* spp.), capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). Lewis and Zwickel (1982) found that yearling blue grouse had increased survival to the next year relative to older birds. Greater sage-grouse (*C. urophasianus*) males exhibit similar survival patterns (Braun 1979, Zablan et al. 2003). Emmons and Braun (1984) reported that all radiomarked yearling ($n = 17$) greater sage-grouse switched leks on average 2.8 times during the breeding season, presumably seeking open territories. This suggests that yearlings spend most of the first spring sampling (Emmons and Braun 1984) and have significantly greater survival than older birds (Braun 1979, Zablan et al. 2003). Data on annual survival rates of capercaillie in these age-classes are sparse (Moss 1987). Moss (1987) suggested that mortality of older birds was slightly (~10%) elevated as compared to yearlings but was not statistically different. Angelstam (1984) reported that radiomarked male black grouse yearlings all survived the breeding and summer season, but older birds suffered higher mortality rates. How, then, does local survival relate to reproductive effort and mating systems?

Little information is available on the breeding behavior of the lesser prairie-chicken (Haukos and Smith 1999). However, from studies of its congeners it is well established that the majority of copulations are performed by a few adult males (≥ 2 yrs of age), and a smaller portion of copulations are secured by yearlings (Hamerstrom and Hamerstrom 1973, Robel 1970, Gratson et al. 1991). Generally, prairie grouse males that

hold peripheral territories acquire fewer copulations than central males (Robel 1970, Gratson et al. 1991). Robel et al. (1970) found that interlek movements of non-territory holding adult greater prairie-chickens occurred at low frequencies, but were common among yearlings. Sharp-tailed grouse (*Tympanuchus phasianellus*) males that held peripheral territories (mostly yearlings) had slightly higher return rates (39 %) than those of centrally located males (33 %) (Gratson et al. 1991). Gratson et al. (1991) also noted the presence of a highly mobile subpopulation of 'non-lekking' males that was mostly yearlings. From Robel et al. (1970) and Gratson et al. (1991) it can be suggested that the frequency of movement between leks may serve as an index to breeding activity. Although, the within season interlek movements of adults and yearlings in my study were equivalent (~17 %), the annual switching of leks by yearlings (20 %) suggests that more sampling was occurring than was detected, and it is possible that yearlings increase their survival rate by reducing the time defending or acquiring territories. Thus, lesser prairie-chicken males appear to fit Wiley's (1974) hypothesis of delayed breeding and increased survival.

Age-specific patterns in reproduction are most pronounced in the more sexually dimorphic grouse species, blue grouse, sage-grouse, and capercaillie. Lewis and Zwickel (1982) found that yearling blue grouse forego reproduction in the first year. Greater sage-grouse exhibit similar survival (Braun 1979, Zablan et al. 2003) and reproductive patterns (Wiley 1974, Hartzler and Jenni 1988). The delayed breeding tactics of yearling capercaillie and sage-grouse are well known (Storch 2001), and males do not achieve complete adult breeding plumage until ≥ 2 breeding seasons. This strategy presumably provides for higher reproductive success as an older bird.

Wiley's (1974) predicted patterns of survival and breeding effort in grouse were supported by the relatively few studies that documented (or could be gleaned from reported returns) age-specific survival and breeding effort (Table 6). Risk modeling of the lek breeding great snipe (*Gallinago media*) indicated that individuals with low reproductive probabilities spent more time hiding than individuals with higher reproductive probabilities (Kalas et al. 1995). This translated into higher survival rates for individuals not participating as frequently in breeding activities. Alternatively, long-lived species such as long-tailed manakins (*Chiroxiphia linearis*) exhibit the opposite pattern where the most successful breeders (birds > 5 yrs old) with high site fidelity had the highest survival rates (McDonald 1993). However, manakins are much longer lived resulting in a different life history strategy. The observed pattern of survival and fidelity in my study correspond to a life-history strategy of a relatively short-lived promiscuous species. The monogamous grouse species (*Lagopus* spp. and *Bonasa bonasia*) tend to have similar survival rates between yearlings and older males, and both breed (Martin et al. 2000, Montadart and Leonard 2002). This does not suggest that all yearlings breed (Hannon and Smith 1984), but when territory holders were removed, yearlings occupied vacant territories (Martin and Hannon 1987).

In some studies, the benefit of maintaining a territory determines over-winter survival of males (Jenkins et al. 1963, Pedersen 1984). Although, fall territory ownership is only directly related to over-winter survival of red grouse males (*Lagopus lagopus scoticus*), territory ownership in general conveys higher fitness of other ptarmigan species. Thus, it would appear that the benefits of reproducing in the first year outweigh the potential costs to future survival in monogamous species.

In conclusion, I observed age-dependent effects for lek fidelity and local survival. It was surprising that yearling lesser prairie-chicken males survived at a higher rate than older birds; this result was contrary to studies of most other birds. The observed pattern in survival rates were not likely biased by emigration rates, because the interlek movement data demonstrated greater movements among yearling than adults. Therefore variation in local survival is likely due to changes in true survival and the observed patterns could be even more pronounced, because local survival is more likely to be an underestimate of true survival for yearlings. These age-specific patterns are perhaps more pronounced in lek mating grouse than other mating systems, where male-male competition is reduced. Lesser prairie-chickens in southwest Kansas fit models of bimaturism in survival and breeding effort, but further work is needed to model survival with age and direct measures of reproductive effort as covariates.

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Table 1. Numbers of adult and yearling lesser prairie-chicken males captured for the first time (F) or recaptured (R) from a previous year, and trapping efforts in Finney County, Kansas.

Year	No. leks	Trap days ^a	Days/lek (SD)	No. adults		No. yearlings		Totals	
				F	R	F	R	F	R
1998	6	68	11.3 (1.5)	44	ND ^b	50	ND	94	ND
1999	8	62	7.8 (4.5)	26	6	23	15	49	21
2000 ^c	20	138	6.9 (1.6)	85	5	52	11	137	16
2001	19	137	7.2 (0.5)	59	45	48	36	107	81
2002	19	143	7.5 (1.2)	38	26	38	31	76	57
Overall		548	7.9 (1.7)	252	82	211	93	463	175

^a The number of days a set of walk-in funnels was placed on a lek.

^b ND = no data.

^c Trapping was conducted on Areas I and II during 2000 to 2002.

Table 2. Age-specific mark-recapture modeling for male lesser prairie-chickens in Finney County, Kansas, 1998-2002.

Model structure ^b	Model statistics ^a				
	AIC _c	ΔAIC _c	w_i	<i>Dev</i>	<i>K</i>
$\phi^1_{\text{age}+\text{t}}, \phi^2_{\text{c}}, p_{\text{c}}$	653.92	0.00	0.749	22.93	7
$\phi_{\text{t}}, p_{\text{c}}$	657.70	3.77	0.113	30.82	5
$\phi^1_{\text{t}}, \phi^2_{\text{c}}, p_{\text{c}}$	658.63	4.71	0.071	29.71	6
$\phi^1_{\text{age}*\text{t}}, \phi^2_{\text{c}}, p_{\text{c}}$	660.09	6.17	0.034	22.85	10
$\phi^1_{\text{age}*\text{t}}, \phi^2_{\text{t}}, p_{\text{c}}$	661.03	7.10	0.022	19.58	12
$\phi^1_{\text{age}*\text{t}}, \phi^2_{\text{t}}, p_{\text{t}}$	662.67	8.75	0.009	16.97	14
$\phi^1_{\text{age}}, \phi^2_{\text{c}}, p_{\text{c}}$	670.54	16.62	0.000	45.72	4
$\phi^1_{\text{c}}, \phi^2_{\text{c}}, p_{\text{c}}$	672.12	18.20	0.000	49.33	3
$\phi_{\text{c}}, p_{\text{c}}$	678.41	24.48	0.000	57.64	2

^a Model fit is described with deviance (*Dev*), the number of parameters (*K*), Akaike's Information Criterion corrected for small sample size (AIC_c), and AIC weights (w_i). The candidate models are presented including the global model, $\phi^1_{\text{age}*\text{t}}, \phi^2_{\text{t}}, p_{\text{t}}$.

^b Models were structured to separate local survival for yearlings and adults (age) immediately after banding (ϕ^1), local survival in later transitions (ϕ^2), and recapture rates (p). Factorial models (*) included main effects and interaction with time; additive models (+) included main effects only. Time dependence (t) in a given model is annual variation in rates.

Table 3. Local survival rates and recapture probabilities for male lesser prairie-chickens separating survival immediately after first capture from later transitions, Finney County, Kansas, 1998-2002.

Year	$\hat{\phi}$ after 1 st capture \pm SE		$\hat{\phi}$ in later years \pm SE		$\hat{p}_c \pm$ SE
	Yearling	Adult	Adult		Both
1998-99 ^a	0.508 \pm 0.089	0.320 \pm 0.079	ND ^b		0.740 \pm 0.066
1999-00	0.390 \pm 0.097	0.226 \pm 0.071	0.272 \pm 0.094		0.740 \pm 0.066
2000-01	0.810 \pm 0.071	0.661 \pm 0.081	0.564 \pm 0.143		0.740 \pm 0.066
2001-02	0.593 \pm 0.095	0.400 \pm 0.081	0.312 \pm 0.060		0.740 \pm 0.066
Overall ^c	0.615 \pm 0.068	0.485 \pm 0.058	0.347 \pm 0.047		0.734 \pm 0.067

^a Annual variation of local survival ($\hat{\phi}$) estimates were derived from the model $\phi^1_{age * t}, \phi^2_t, p_c$.

^b ND = no data.

^c Overall means were derived from the model $\phi^1_{age}, \phi^2_c, p_c$.

Table 4. The numbers of within- and between-year interlek movements of banded male lesser prairie-chickens, Finney County, Kansas, 1998-2002.

Capture interval	Movement ^a	Between Years		Within years	
		Yearling	Adult	Yearling	Adult
1-2	No	48 (0.80) ^b	60 (0.92)	34 (0.83)	41 (0.82)
1-2	Yes	12 (0.20)	5 (0.08)	7 (0.17)	9 (0.18)
2-3	No	9 (0.69)	11 (1.0)	23 (0.92)	14 (0.94)
2-3	Yes	4 (0.31)	0	3 (0.08)	1 (0.06)
3-4	No	1	0	0	7
3-4	Yes	1	0	0	1
4-5	No	0	0	3	2
4-5	Yes	0	0	0	1
Totals					
	No	58 (0.77)	71(0.93)	60 (0.86)	66 (0.85)
	Yes	17 (0.23)	5 (0.07)	10 (0.14)	12 (0.15)
<i>P</i> -value ^c		0.004		0.851	

^a Movements are described as a bird recaptured at least once on a lek other than the first lek of capture.

^b Number and proportion (in parentheses) of individuals recaptured on leks within an age-class (column).

^c The *P*-value was estimated using a likelihood ratio (*G*) test on a 2 × 2 contingency table (yearling/adult: move/not-move), df =1, between years *G*= 8.222, and within years *G* = 0.035.

Table 5. Estimates of survival for North American prairie grouse (*Tympanuchus* spp.) obtained from live encounters (B), dead recovery (R), known-fate telemetry (T), and age-ratios from wing (W) analyses.

Species	Mark type	Model type ^a	Sex ^b	Survival	Reference
LPCH ^c	B	CJS	M	0.46	This Study
LPCH	R	LFT	M	0.32	Campbell (1972)
LPCH	T	K-M	M	0.57	Jamison (2000)
GPCH ^c	B	LFT	M	0.48	Hamerstrom and Hamerstrom (1973)
SHTG ^c	B	LFT	M	0.50	Amman (1957)
SHTG	R	LFT	U	0.25	Robel et al. (1972)
SHTG	B	PRP	M	0.17	Moyles and Boag (1981)
SHTG	B	PRP	M	0.36	Gratson et al. (1991)
SHTG	T	K-M	U	0.57	Schroeder (1997)
SHTG	W	PRP	U	0.56	Giesen (1999)
SHTG	T	K-M	M	0.35	Boisvert (2000)

^a Model types are as follows: CJS = Cormack-Jolly-Seber, K-M= Kaplan-Meier, LFT = life-table analysis, and PRP = the proportion of survivors reported.

^b Studies that were male specific Sex = M, and in those that did not differentiate gender in estimates Sex = U.

^c LPCH = *T. pallidicinctus*, GPCH = *T. cupido*, SHTG = *T. phasianellus*

Table 6. Estimates for age-specific survival and breeding for male grouse obtained from live encounters (B), dead recovery (R), known-fate telemetry (T), and age-ratios from wing (W) analyses.

Mating system / species	Model type ^a	Data	Age / survival rate				Delayed maturation	
			1 ^b	2	≥2	Ref ^c	Y	Ref ^c
Monogamous								
Willow ptarmigan	PRP	B	0.44	ND ^d	0.25	5	N	5,17
Rock ptarmigan	PRP	B	0.24	ND	0.21	1	N	1
White-tailed ptarmigan	LFT	B	0.76	0.74	0.30	3	N	3
Hazel grouse	K-M	T	0.75	ND	0.75	21	N	18
Dispersed arena								
Ruffed grouse	PRP	B	0.41	0.42	0.44	4	Y	4
Siberian spruce grouse	ND	ND	ND	ND	ND		Y	19
Spruce grouse	PRP	B	0.92	ND	0.81	9	Y	15
Blue grouse	PRP	B	0.55	0.84	0.75	11	Y	11
Lek mating								
Greater prairie-chicken	LFT	B	0.50	0.48	0.41	7	Y	6,7
Lesser prairie-chicken	CJS	B	0.62	0.49	0.35	23	Y	23
Sharp-tailed grouse	PRP	B	0.39	ND	0.33	16	Y	10, 16
Black grouse ^e	K-M	T	1.0	ND	0.70	9	Y	2
Greater sage-grouse	REC	B	0.63	ND	0.37	22	Y	8,14
Capercaillie	PRP	W	0.54	ND	0.46	13	Y	20

^a Model types are as follows: CJS = Cormack-Jolly-Seber, K-M= Kaplan-Meier, LFT = life-table analysis, and PRP = the proportion of survivors reported.

Table 6. continued

^b Age of birds 1 = yearling, 2 = 2 years old (adult in this study), and ≥ 2 = 2 years old or older (older adult in this study).

^c References: 1, Weeden (1965); 2, Kruijt and Hogan (1967); 3, Braun (1969) 4, Gullion and Marshall (1968); 5, Bergerud (1970); 6, Robel (1970); 7, Hamerstrom and Hamerstrom (1973); 8, Wiley (1974); 9, Keppie (1979); 10, Moyles and Boag (1981); 11, Lewis and Zwickel (1982); 12, Anglestam (1984); 13, Moss (1987); 14, Hartzler and Jenni (1988); 15, Szuba and Bendell (1988); 16, Gratson et al. (1991); 17, Martin (1991); 18, Swenson (1991); 19, Andereev et al. (2001); 20, Storch (2001); 21, Montadert and Leonard (2002); 22, Zablan et al. (2003); 23, This study.

^d ND = no data available.

^e Survival estimates were for breeding and summer season only.

CHAPTER 2

RADIOTELEMETRY ESTIMATES OF SURVIVAL IN THE LESSER PRAIRIE-CHICKEN: ARE THERE TRANSMITTER BIASES?

Abstract: Radiotelemetry has provided wildlife biologists with a tool to estimate survival where fate of each individual is likely known. Whereas analyses of these data can result in highly accurate estimates, 5 assumptions must be met. Two of these assumptions, that right-censoring is random with respect to the survival of study animal, and that transmitters have no effect on survival of study animal, are often difficult to assess. Using joint models developed for live encounter and dead recovery data, I examined the potential for bias in survival estimates of radiomarked male lesser prairie-chickens in southwestern Kansas. Additionally, I use graphing techniques to assess if the assumption of random censoring holds in this study. In total, 201 male lesser prairie-chickens were captured and marked during this study. Seventy-five of these birds were fitted with radios (68 survived a 2-week acclimation period) and 126 were in the banded group. Model selection and parameter estimation were based on the information theoretic-approach. The model best supported by the data, $S_c, p_{group+t}, r_g, F_c$, indicated that survival was best modeled as constant ($\hat{S}_c = 0.731$, SE = 0.072) across radiomarked and banded birds. Signal loss occurred throughout the monitoring period and appeared to be independent of periods of high mortality. Eight of 16 (50.0, SE = 1.6 %) right-censored birds were subsequently recaptured, which was similar to the recapture rates for known-fate birds (23 of 52; 55.8%, SE = 0.5 %), indicating that right-censored birds had similar survival rates to that of known-fate individuals.

INTRODUCTION

Radiotelemetry is widely used to collect data for estimating survival rates of experimental treatments or groups in wildlife studies. Unbiased survival estimation requires meeting several fundamental assumptions, 1) radioed animals are representative (random and independent samples) of the population of interest, 2) observation periods (or locations) are independent, 3) working radios are always located, 4) censoring is random (i.e., any animal not located is as likely to be alive as dead), and 5) radios do not impact survival of marked individuals (Winterstein et al. 2001). Assumptions 1 to 3 can be met by implementing the appropriate research design. Assumptions 4 and 5 are less controllable as the vagaries of equipment and behavior of individual animals cannot be accounted for entirely in project design. However, assumptions 3 and 4 are closely related as undetected individuals (i.e., vagaries of equipment) will be right-censored for a given period. Right-censoring occurs when an individual “leaves” a study either temporarily or permanently and the fate of the individual is unknown. Thus, all individuals are “right-censored” at the termination of a project because, by definition, their fate beyond that point is unknown. In practice animals are right-censored when there is radio failure, detection rates are < 1 , or there is emigration from the study area. Often the detection of a working radio depends on the length of the observation period, and proper planning of a project can increase the likelihood of meeting assumption 3. Generally, researchers are faced with accepting assumptions 4 and 5 without controls to test their validity or impact (Esler et al. 2000).

The effect of radio transmitters on survival on game birds has been well-studied, but the results have been mixed. Most studies suffer from a lack of a suitable control

group and rigorous estimates of survival. Typically studies examine differences in return rates or daily survival of birds marked with 2 or more types of harness configuration or transmitter mass. Several studies on upland game birds provided evidence suggesting that radios with external attachments (e.g., poncho, necklace, and backpack) had negative impacts on survival (see review by Withey et al. 2001). In contrast, other study designs have found no measurable effect of radios on survival or other vital rates (Hines and Zwickel 1985, Cotter and Gratto 1995, Thirgood et al. 1995, Bro et al. 1999). Handling effects (i.e., increased mortality immediately after handling) have occurred with early radio designs (Marks and Marks 1987, Pekins 1988). However, the studies mentioned above examined return rates as a measure of survival. Unfortunately return rates are confounded by 4 probabilities: true survival (S), site fidelity (F), site propensity (γ^*), and detection (p^*). Mark-recapture models can provide survival estimates while accounting for fidelity and detection rates. However, return rates can be biologically meaningful when a species exhibits fidelity to trapping areas (Esler et al. 2000). Currently, no studies have examined the effects of radiomarking using contemporary analyses of capture-recapture.

I examined the potential effect of radiomarking on survival of male lesser prairie-chicken (*Tympanuchus pallidicinctus*) using a novel approach of live-recapture dead recovery models. Typically, joint-analyses of live and dead recoveries (Burnham 1993) have been applied to banded individuals marked-recaptured on breeding grounds and possibly recovered during the hunting season. I expanded these joint-analyses to include live capture and recapture of banded and radiomarked (i.e., physical recapture or detection of transmitter signal from live radiomarked birds) individuals, and dead

recovery of hunter-harvested (both banded and radiomarked) and mortalities of radiomarked individuals. I also examined the potential bias of right-censoring by comparing the return rates of known-fate and right-censored individuals.

METHODS

Trapping, marking, monitoring

This study was conducted in native sand sagebrush prairie south of Garden City, Kansas (37° 52' N, 100° 59' W) from spring 1998 to spring 2000. Lesser prairie-chickens were captured over 3-week periods using walk-in funnel traps on leks during spring (in late Mar to Apr) and fall (late Sep to Oct) (Haukos et al. 1991, Salter and Robel 1999). Both females and males were captured but recaptures of females were few and this study examines only the male cohort of the radiomarked population. Captured birds were marked with serially numbered aluminum leg bands. Relatively equal numbers of birds were marked at all leks ($n = 11$) to ensure relatively equal sampling across the study site. Birds were fitted with necklace-style radios with a mass ≤ 12 g; $\leq 1.7\%$ of a male's body mass ($\bar{x} = 790$ g, range = 700 - 950 g). The radio transmitters had 8-month battery-life, whip antennae, and 8 hr mortality switch. All birds that did not survive 2-weeks post-capture (i.e., acclimation period) were included in the analysis. This conservative approach allowed for acute effects of transmitters to be considered. Radiomarked birds were monitored daily using a truck-mounted null-peak antenna system to ascertain their status. For purposes of this study, the observation period was 6 months for radiomarked birds.

Data analysis

I used a joint analysis for mark-recapture and staggered-entry known-fate data from radiotelemetered and banded birds using live-recapture dead-recovery models (hereafter joint models) (Burnham 1993) to examine the effects of radiomarking on lesser prairie-chicken survival. My analysis included 5 encounter occasions (5 6-month intervals between April 1998 and April 2000) and 2 attribute groups (banded or radiomarked). Radiomarked individuals that survived a given interval and had their radio removed at recapture ($n = 11$) were right-censored from the radiomarked group and added to the banded group, and the opposite was true for banded birds that received a radio at a subsequent interval ($n = 5$). When a radio signal was lost prior to a capture period (i.e., prior to the expected life of the transmitter) they were treated as a removal from the encounter history and right-censored.

Joint models of survival allow for combination of multiple sources of information (Burnham 1993, Barker and White 2001). In my study, these sources of live encounter come from 5 standard mark-recapture periods (once every 6 months) of banded birds, “resighting” (p) periods of live radiomarked individuals, and reporting periods (r) of both banded and radiomarked birds. Although hunter reporting of banded birds did occur, this proportion was $< 5\%$, but this information was included in the analysis. Thus, a radiomarked individual may be alive and encountered, but not physically recaptured at a given encounter period. Joint models necessarily are more complex than Cormack-Jolly-Seber (CJS) models of live capture data (Burnham 1993). The parameters and their definitions are as follows:

S_i = The probability of survival; i.e., an animal that is alive at time i , is again alive at time $i + 1$.

p_i = The probability of detection; i.e., an animal that is alive, is at risk of capture at trapping occasion i is captured.

r_i = The probability of reporting; i.e., a marked animal that is alive at time i dies is reported at time $i + 1$.

F_i = The probability of site fidelity; i.e., an animal that is at risk of capture at trapping occasion i and is again at risk of capture at time $i + 1$.

Joint models of survival of banded and radiomarked individuals were analyzed following three steps: 1) selection of the global model, 2) goodness-of-fit tests (GOF), and 3) development of less parameterized models and model selection. Model selection criterion was based on either Akaike's Information Criterion adjusted for small sample sizes (AIC_c), or the quasi-likelihood corrected version of AIC_c (QAIC_c). Protocols of Burnham and Anderson (1998) were followed to identify the model best supported by the data. Model development and parameter estimation was conducted in MARK 3.0 (White and Burnham 1999) using design matrices and the logit link function.

I developed an *a priori* set of candidate models (Table 1) that allowed me to examine the potential for the effects of radiomarking. My primary interest was evaluating survival (S); thus, recapture (p), reporting (r), and fidelity (F) were considered nuisance parameters. Subscripts following parameters indicate explanatory variables (e.g., $S_{\text{group} \times t}$ describes a model that includes both marker effect (i.e., group = marker type banded or radiomarked) and time-dependence (i.e., survival varies by encounter occasion) in survival. Subscript (handle) denotes different survival rate for the interval

after initial release or all subsequent intervals, respectively. Lastly, I used (c) to describe models with parameters held constant (e.g., S_c , describes a model where survival is held constant). I fitted alternative structures of F , r , and p to the global model ($S_{group*t}, p_{group+t}, r_{group}, F_c$) that were biologically and practically meaningful. I fixed the parameter $F_c = 0.979$ as only 2 of 95 (0.979) radiomarked males were known to have permanently emigrated. Because few banded birds were reported dead, I did not consider time-dependence in r . I assumed that behavioral differences in seasons would lead to consistently unequal capture probabilities, p , between fall and spring encounters (Salter and Robel 1999), and additive time structure was assumed for p under the global model. Subsequently, time (t) and group ($group$) structures were fitted to p and the best structure was selected based initially on minimum AIC_c. Given that the detection probabilities in p and r of radiotelemetry (~ 1) and banding data (< 1) were unequal, I identified a limited number of structures for these parameters. Specifically I did not consider models with p and r held constant. The simplest form was with a group effect only. Survival of radiomarked and banded birds was examined as a group effect (S_{group}). An alternative model structure was fit to examine potential differences in handling effect for both marker types ($S_{group, handle}$). This model allowed survival to vary by group effect, and for the interval of capture to be different from later encounters.

The overall GOF of the global model was assessed using the parametric bootstrap in MARK. The proportion of simulations ($n = 1,000$) that had a greater deviance than the observed deviance provided an assessment of model fit. If this proportion was small (< 0.05) then this provides evidence that the model fits the data poorly (Cooch and White 2001). I used these simulations to estimate the degree of overdispersion (\hat{c}), by dividing

the observed deviance by the bootstrapped mean deviance. If the global model had a poor fit, and $\hat{c} < 3$, then AIC_c was adjusted accordingly to this derived value of \hat{c} , and $QAIC_c$ used for model selection (Anderson et al. 1994).

I examined the assumption of random censoring by comparing return rates of known-fate individuals (number alive and recaptured / number alive + number dead) were compared to the proportion of birds that initially were right-censored, but were recaptured or reported later (number censored and recaptured / total number censored). I constructed a 95% confidence interval around the difference of these proportions to determine if it was different from 0 (Agresti 1996).

I calculated an effect size (i.e., difference of means) and its 95% confidence interval to determine if body masses differed between the 2 groups. I report sample sizes and standard deviation along with the effect size.

RESULTS

A total of 201 male lesser prairie-chickens was captured and marked during this study. Seventy-five of these birds were fitted with radios (68 survived the 2-week acclimation period), and 126 were in the banded treatment group. Fall trapping resulted in fewer birds captured per unit effort than spring trapping (Salter and Robel 1999), and this was evident in the group and time additive (*group + t*) parameter structures in the model selection below. Treatment groups were similar with respect to body mass and age-classes. Body mass of radiomarked ($n = 72$, $\bar{x} = 790$, $SD = 48$ g) and banded ($n = 133$, $\bar{x} = 803$, $SD = 44$ g) birds was similar (\bar{x} difference = -12.2 , $CI: -25.5, 1.1$ g) as was the proportion of yearlings to adults in each sample, 0.83 and 0.79, respectively.

The fit of the global model ($S_{group*t}, p_{group+t}, r_g, F_c$) was rejected by the parametric bootstrap ($P < 0.001$), but was retained because overdispersion was minor $\hat{c} = 2.382$. Model selection and inference were made from QAIC_c (Anderson et al. 1994). Some of the overdispersion may have been due to a lack of independence, as some individuals were in both the banded and radiomarked groups.

The model best supported by the data, $S_c, p_{group+t}, r_g, F_c$, indicated that survival was best modeled as constant ($\hat{S}_c = 0.742$, SE = 0.065) across radiomarked and banded birds. There was some model uncertainty as $\Delta\text{QAIC}_c < 2$ for the top 3 models, which suggested that handling, $S_{handle}, p_{group+t}, r_g, F_c$ ($\hat{S}_1 = 0.704$, SE = 0.086; $\hat{S}_2 = 0.797$, SE = 0.114), and group effects, $S_{group}, p_{group+t}, r_g, F_c$ ($\hat{S}_{radio} = 0.761$, SE = 0.069; $\hat{S}_{band} = 0.671$, SE = 0.112) may have been present (Table 1). The survival estimates from model averaging indicated that radiomarked individuals had slightly higher survival ($\hat{S}_{radio} = 0.745$, SE = 0.073) than banded birds ($\hat{S}_{band} = 0.711$, SE = 0.090). Reporting rates were higher for radiomarked birds ($r = 0.636$, SE = 0.157) than banded birds ($r = 0.103$, SE = 0.057). Recapture probabilities varied additively over time for both groups (Table 2), and, radiomarked birds had higher overall recapture rates ($p_{radio} = 0.645$, SE = 0.120; $p_{band} = 0.303$, SE = 0.124).

Effects of right-censoring

Radio signals were permanently lost for 16 birds during the 6-month sampling intervals and were right-censored. An additional 24 radio signals were lost after the 6-month battery life expired, and were detected as alive at last encounter occasion (this accounts for part of known-fate percentages). Signal loss occurred throughout the monitoring period and appeared to be independent of periods of high mortality (Fig. 1).

Eight of 16 (50.0, SE = 1.6 %) right-censored birds were subsequently recaptured, which was similar (% difference = -5.8; CI: -33.8, 22.2 %) to the recapture rates for known-fate birds (23 of 52; 55.8%, SE = 0.5 %), suggesting that right-censored birds had similar survival rates to that of known-fate individuals.

DISCUSSION

This study found no evidence that radiomarking male lesser prairie-chickens negatively impacted their survival. Rather, contrary to the predicted outcome, radiomarked individuals had a slightly higher survival rate. Right-censored birds had similar return rates when compared to those with known-fates. Inference about survival in this group was based on relatively small sample sizes but return rates were similar enough to provide support for a comparable mortality rate between them. I recognize that my analyses were retrospective and an experimental design would have had greater statistical power. However, given the positive direction of the difference between radiomarked and banded birds, it is likely that radios had little impact on bird survival in my study population. Inference in this study is limited to the male cohort of the population. However, given that females average about < 70 g males, it is likely that small transmitters (<12 g) have little impact on their survival.

Two types of transmitters

This is the first study to demonstrate that radios had no measurable effect on prairie grouse (*Tympanuchus* spp.). Previous work on both sharp-tailed grouse (*T. phasianellus*) and greater prairie-chickens (*T. cupido*) detected large negative effects of radios on survival (Marks and Marks 1987, Burger et al. 1991). It is important to note that Marks and Marks (1987) and Burger et al. (1991) measured the effects of the larger

(18-22 g) poncho-style solar powered transmitters, in contrast to the 12-g lithium battery-powered necklace style used in my study. Marks and Marks (1987) lacked a suitable control group ($n = 9$) to compare return rates or survival with the radiomarked birds ($n = 36$). However, 23 of 35 radiomarked birds in the Marks and Marks (1987) study succumbed to predation, of which 65% occurred during the breeding season. Burger et al. (1991) documented that birds marked with larger 2-stage transmitter and reflective surface had twice the probability of being depredated than those fitted with 1-stage radios (14 g). Similar patterns of mortality were documented for ruffed grouse (*Bonasa umbellus*) and ring-necked pheasant (*Phasianus colchicus*), where birds marked with a heavier backpack style transmitters had reduced survival rates (Warner and Etter 1983, Small and Rusch 1985).

Two types of marking

Thirgood et al. (1995) found no measurable effect of radiomarking (necklace style transmitters) on red grouse (*Lagopus lagopus scoticus*) when compared to patagium tagged birds. They suggested that the miniaturization of the necklace-style transmitters has alleviated some of the lethal effects reported earlier in other grouse species with larger transmitters (Marks and Marks 1987, Pekins 1988). Thirgood et al. (1995) suggested that necklace style transmitters are the preferred method for marking grouse species. Alternatively, Caizergues and Ellison (1998) reported lower nest success rates and smaller brood sizes of radiomarked black grouse (*Tetrao tetrix*) females when compared to unmarked individuals, but they did not examine survival rates. Overall, radiomarked females raised fewer broods than unmarked birds, but chicks per female were nearly equal between the 2 groups (Caizergues and Ellison 1998). One limitation to

their study was that individuals were not individually identifiable in their unmarked population. Thus, larger brood sizes could have been an artifact of double counting females with large broods. The marked sample was relatively small (≤ 8 marked females per year, $n = 26$ for 5 years), thus detecting annual differences in reproductive success between groups was not possible.

The cause of marker-specific survival rates may not be easily understood as yearly variation can impact the outcome of these studies (Cotter and Gratto 1995, Bro et al. 1999). Years when birds may be stressed or in poor condition may increase the negative effect of radiomarking. In my study, models with time dependency (i.e., either $S_{group+t}$ or $S_{group*t}$) in survival were not supported by the data. Although the additive models had slightly better fit than full time-dependence, they indicated that radioed birds on average had higher survival than banded birds.

Censoring

Random censoring is a critical assumption of telemetry studies, and violation of the assumption can result in significant bias in \hat{S} (Tsai et al. 1999, Winterstein et al. 2001). This assumption has been difficult to evaluate in the field (Esler et al. 2000). In this study, return rates were similar between known-fate and right-censored individuals, and the timing of censoring appeared to be independent of mortality (Fig. 1). However, the power of my retrospective study to detect even a 10 % difference in return rates was low ($\beta = 0.11$). Esler et al. (2000) documented a similar pattern in radiomarked harlequin ducks (*Histrionicus histrionicus*) but also acknowledged the low power of their study design.

Miniaturization and method of attaching transmitters appear to have reduced the impact of radios on survival of prairie grouse, because survival rates of radioed birds in my study were higher than those reported by Marks and Marks (1987) and Burger et al. (1991). Male lesser prairie-chickens in my study were not measurably impacted by radiomarking, as their survival rates were greater than or equal to those of banded birds. Inference was limited to the male cohort of this population. Future work should implement a rigorous experimental study to examine the effects of transmitters on free-living birds and females under field conditions.

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Table 1. Candidate live-dead recovery models for estimating survival of radiomarked and banded lesser prairie-chickens in Finney County, Kansas, 1998-2000.

Model structure ^b	Model statistics ^a				
	QAIC _c	ΔQAIC _c	w_i	K	Dev
$S_{c,p_{group+t}, r_{group}, F_c}$	279.5	0.00	0.43	8	77.81
$S_{c,handle, p_{group+t}, r_{group}, F_c}$	280.8	1.36	0.22	9	77.04
$S_{group, p_{group+t}, r_{group}, F_c}$	281.1	1.65	0.19	9	77.33
$S_{group,handle, p_{group+t}, r_{group}, F_c}$	282.5	3.02	0.09	10	76.55
$S_{t,p_{group+t}, r_{group}, F_c}$	284.9	5.42	0.03	12	74.62
$S_{group+t, p_{group+t}, r_{group}, F_c}$	286.2	6.72	0.01	13	73.73
$S_{group*t, handle, p_{group+t}, r_{group}, F_c}$	287.9	8.37	0.01	18	64.23
$S_{t,handle, p_{group+t}, r_{group}, F_c}$	288.1	8.57	0.01	13	75.58
$S_{group+t, handle, p_{group+t}, r_{group}, F_c}$	288.2	8.70	0.01	14	73.51
$S_{group, handle+t, p_{group+t}, r_{group}, F_c}$	288.6	9.15	0.00	14	73.96
$S_{group*t, p_{group+t}, r_{group}, F_c}$	288.8	9.30	0.00	15	71.89
$S_{group+t, handle+t, p_{group+t}, r_{group}, F_c}$	292.2	12.72	0.00	17	70.84
$S_{group*t, handle+t, p_{group+t}, r_{group}, F_c}$	293.3	13.82	0.00	22	60.48

^a Model fit is described by deviance (Dev), the number of parameters (K), quasi-Akaike's Information Criteria ($\hat{c} = 2.382$) corrected for small sample size (QAIC_c), and QAIC_c weights (w_i).

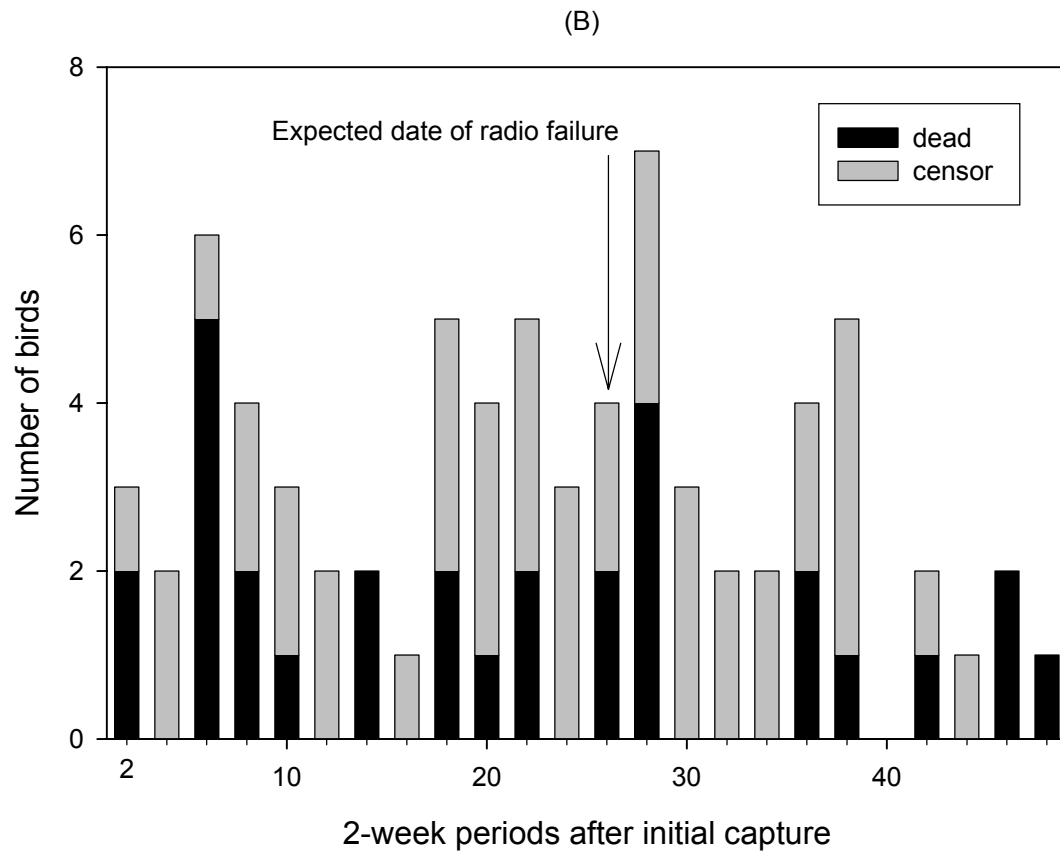
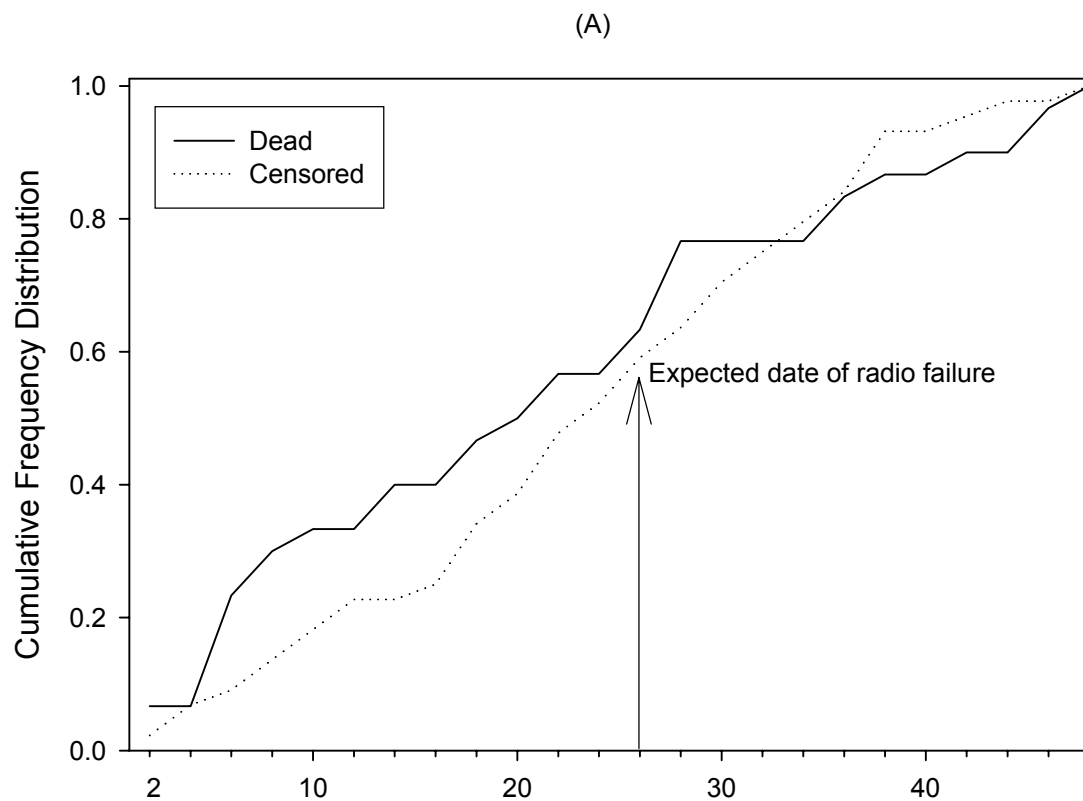
^b Models were structured to separate survival (\hat{S}), for marker effect ($group$) for both radiomarked and banded males immediately after handling ($handle$), and survival in later transitions. Parameter estimates include recapture rate (p), reporting rate (r), and site fidelity (F) which was fixed at 0.979.

Table 2. Model averaged parameter estimates (\pm SE) from the 3 best ($\Delta\text{QAIC}_c < 2$) live-dead recovery models of radiomarked and banded male lesser prairie-chickens in Finney County, Kansas, 1998-2000.

Parameter estimates ^a	Marker type	
	Banded	Radio
S_{group}	0.711 ± 0.090	0.745 ± 0.073
$p_{\text{fall-98}}$	0.161 ± 0.076	0.502 ± 0.129
$p_{\text{spring-99}}$	0.574 ± 0.162	0.876 ± 0.071
$p_{\text{fall-99}}$	0.158 ± 0.084	0.495 ± 0.137
$p_{\text{spring-00}}$	0.318 ± 0.172	0.707 ± 0.145
r_{group}	0.103 ± 0.057	0.636 ± 0.157
F	0.979 ± 0.000	0.979 ± 0.000

^aParameter estimates include survival (\hat{S}), recapture rate (p), reporting rate (r), and site fidelity (F).

Fig 1. The cumulative frequency distribution (A) of mortalities and right-censoring indicates that the high mortality periods (2-week intervals) were not associated with right censoring. The distribution of mortality and right-censoring (B) indicates the actual numbers lost to mortality or signal in a given 2-week period were not usually related. Both figures show time (2-week periods) from capture and release.



CHAPTER 3

GENDER AND AGE-SPECIFIC SURVIVAL AND PROBABLE CAUSES OF MORTALITY IN RADIOMARKED LESSER PRAIRIE-CHICKENS IN KANSAS

Abstract: Long-term declines in population indices and reductions in habitat have lead to increasing concern over the status of the lesser prairie-chicken (*Tympanuchus pallidicinctus*). It is essential to identify management approaches that have the greatest positive impact on rates of population growth. I evaluated the effects of season, age, and gender on the survival of lesser prairie-chickens in southwestern Kansas. Using data from a 6-year field study, I estimated summer (Apr - Nov) and seasonal rates (Apr - Mar) using known-fate (radiotelemetry) survival models. I evaluated the probable mortality causes of radiomarked birds. In total, 136 male (46 yearling, 66 adult, 24 age undetermined), and 227 female (87 yearling, 117 adult, and 23 age undetermined) lesser prairie-chickens were captured and fitted with radio transmitters from 1997 to 2002. The summer known-fate analyses revealed that overall male ($\hat{S} = 0.71$, SE = 0.06) and female ($\hat{S} = 0.69$, SE = 0.06) survival rates were similar, but females were most susceptible to mortality during May and June. Additionally, the summer analysis indicated that yearling females had a greater probability ($\hat{S} = 0.77$, SE = 0.06) of surviving than adults ($\hat{S} = 0.62$, SE = 0.05). These patterns were consistent for both the seasonal and summer survival rates. One-hundred and thirty-four mortalities were recorded from spring 1997 to spring 2003, and 54% were attributed to mammalian predation. Generally, lesser prairie-chickens had higher estimated survival than those reported for other prairie grouse, suggesting that adult survival was not a limiting factor for lesser prairie-chickens in Kansas.

INTRODUCTION

Seasonal survival (S) rates and the timing of mortality ($1 - S$) events are important parameters in evolutionary ecology and wildlife management (Caizergues and Ellison 1997). Understanding the seasonal variation in the timing of mortality and its severity are especially important to grouse management (Bergerud 1988), as females in promiscuous systems (unipaternal care) may have an increased mortality risk during incubation and brood-rearing periods. Yearling and adult females may have different survivorship based on reproductive effort and success (Saether 1990). In general, more experienced birds will have greater fecundity and survival, thus resulting in lower yearling survival rates (Saether 1990).

Male and female grouse of promiscuous mating systems have different reproductive costs. Males do not participate in nest-building, incubation, or brood-rearing, their only contribution is gametes. However, males do incur a cost of breeding because of conspicuous plumage and displays during territorial defense and may suffer higher mortality than females. Females incur a cost of reproduction through egg production, incubation, and brood rearing. Their susceptibility to predation during incubation is thought to be higher than other times of year (Bergerud 1988). It is unclear if a short-term decrease in female survival (reproductive cost) would yield a lower annual survival rate than males. Is it possible that the cost of nesting and conspicuous display will result in similar survival rates between the genders?

Differential survival in gender and age-classes may result in either skewed sex- or age-ratios in harvest (e.g., wing or head samples) or count data (Amman 1957, Campbell 1972, Linden 1981, Moss 1987, Bergerud 1988). Survival estimates from age-ratios

assume stable populations, equal sampling of yearlings and adults, and a constant mortality rate. Most survival estimates for grouse have been based on these methods (Bergerud 1988). Given the tenuous status of many grouse populations (Storch 2000), more accurate estimates are needed for conservation actions. Radiotelemetry may provide accurate parameter estimates if the basic assumptions are met (Winterstein et al. 2001).

Little is known about seasonal or annual survivorship of lesser prairie-chickens (*Tympanuchus pallidicinctus*), but such information is critical for this species of conservation concern. It is currently listed as a “warranted but precluded” threatened species (U.S. Fish and Wildlife Service 2002). Band recovery data from hunters in New Mexico were used to estimate an annual survival rate of 35% (Campbell 1972), and Merchant (1982) estimated a 6-month survival rate of 59% (extrapolated 12-month survival = 35%) for radiomarked females that included the nesting and brood rearing periods. In Kansas, Jamison (2000) estimated annual survival of radiomarked males to be 57%. Six-month (Apr-Sep) survival rates were estimated at 74% for males and females during the same study (Jamison 2000). This estimate extrapolated to 12 months would be approximately 55%. However, lower survival rates of females than males have been implicated in biased sex-ratios (Campbell 1972); there is little evidence to support this idea. The available information on lesser prairie-chicken survival is incomplete, as there are few annual estimates, and no information on the timing of mortality for females and males during a year. Such information is imperative for conservation efforts (e.g., population viability analyses, harvest regulations) and basic ecological understanding.

Using radiotelemetry data from 1997 to 2003, I address 3 research hypotheses and provide a description of probable mortality causes of the lesser prairie-chicken. I examined survival in terms of an overall rate (9 and 12-month periods for males and females) to identify potential cumulative effects of gender-specific costs of reproduction. I quantified the timing of mortality events for males and females to verify the costs of reproduction hypothesis (i.e., did both males and females suffer the lowest survival rates during the breeding season?). Thus, if the cost of reproduction hypothesis is supported then timing may not differ but the overall survival rate will differ. I estimated survival for yearling and adult females to determine if age-structured survival was evident in the population. Here, I test the constraint hypothesis, which argues that yearlings lack some of the skills essential for high reproductive performance. Because high reproductive performance is often linked to survival (Saether 1990), I used survival and ancillary data on reproductive rates to evaluate this hypothesis. Lastly, I evaluated the probable mortality causes of radiomarked birds.

METHODS

Study area

The study region was comprised of 2 fragments (~5000 ha each) of native sandsage (*Artemisia filifolia*) prairie near Garden City, Finney County, Kansas (37° 52' N, 100° 59' W). Work began on Area I (southwest of Garden City) in 1997. In 2000, trapping and monitoring efforts were expanded to include Area II (southeast of Garden City). Prior to 1970, these 2 areas were part of a contiguous tract of native sandsage prairie. The development of center pivot irrigation led to the conversion of much of the sandsage prairie to intensive agriculture (Waddell and Hanzlick 1978), and left these

areas as 2 fragments with about 19 km of agricultural fields between patch centroids (Hullett et al. 1988, Jamison 2000).

Capture, marking, and monitoring

Lesser prairie-chickens were captured on 20 leks using walk-in funnel traps (Haukos et al. 1991, Schroeder and Braun 1991) primarily during spring, and a subset of leks during the fall of 1998 and 1999 for a related study (Salter and Robel 1999, Chapter 2). Spring trapping began the last week of March and continued into the second week of April. Fall trapping lasted approximately 3 weeks in late September and early October. Traps were placed on all known leks (>2 displaying males) found in native prairie on the study sites. Once captured, birds were aged as yearling (~10 months of age) or adult (\geq 22 months) based on shape, wear, and coloration of the 9th and 10th primaries (Amman 1944, Copelin 1963). Age was not recorded during the first year of the study (1997). Gender of mature birds was determined by the patterns on tail and crown feathers (Amman 1944, Copelin 1963). Body mass was measured (\pm 2.5 grams) using a Pesola spring scale.

Birds were individually marked with numbered aluminum leg bands. Radiomarked birds were fitted with a lithium battery-powered necklace-style transmitter (\leq 12-g), which was \leq 1.9 % of a bird's body mass (sexes pooled, \bar{x} = 783, range = 630-890 g) and below the recommended 3 % maximum level (Withey et al. 2001). Transmitters had either an 8- or 12-hour mortality switch, and a 6- (1997-1999) or 12-month (2000-2003) battery life. Nearly all captured females were marked with radio-transmitters, but only a subset of males was marked in a given year. For these samples,

workers attempted to distribute the radios evenly across the study areas, by placing roughly equal numbers on males on each lek trapped.

Radiomarked birds were monitored daily with a vehicle-mounted null-peak twin Yagi antenna system. Once a mortality switch had been activated on a transmitter, the unit was relocated and retrieved with a hand-held Yagi in < 12-hrs. Aerial surveys from fixed wing aircraft were conducted at least once a month to locate undetected signals. Once located by air, previously undetected birds that had emigrated from the primary study areas were subsequently relocated approximately every 10 days from truck-mounted systems.

Probable causes of mortality

When a carcass or kill site was located, the probable cause of mortality was determined as mammal, avian, accident, hunter, snake, or unknown based on the evidence at the recovery site. Scavenging of carcasses was possible but was potentially minimized because of quick recovery of transmitters on a mortality pulse. It is difficult to make unambiguous statements about causes of mortality because of potential scavenging or confounding evidence at a recovery site (Bumann and Stauffer 2002). Thus, I refer to probable causes of mortality in this paper.

A mortality event was classified as mammalian predation if one of the following was evident at the kill site: bite marks on the transmitter, chewed feathers and/or aluminum band in addition to tracks or mammalian scat at the recovery site. Coyote (*Canis latrans*), American badger (*Taxidea taxus*), and bobcat (*Lynx rufus*) were all possible mammalian predators. Carcasses that had been decapitated and/or cleaned of the breast muscle with no apparent chewing, the presence of white wash, or plucking were

classified as avian predation. Accidental deaths were carcasses recovered near a powerline, fenceline, or dismembered by farm machinery that had no apparent marks of predation. Hunter recoveries of banded birds were reported as such. Often these were not radiomarked birds, but are included here to provide an estimate of hunter harvest. Snake predation was rare, but evidenced by feathers matted with saliva or residue from the head to just above the furcula. Unknown causes included mortalities that went undetected for more than 2 days, carcasses with confounding signs at the recovery site (e.g., mammalian chew marks on feathers, etc., and under a powerline), or in the event a carcass was recovered unscathed. Likelihood-ratio tests (G^2) were used to examine the differences in mortality causes between males and females.

Survival modeling

Known-fate survival modeling requires that 6 assumptions be met: the animals marked are a random sample from the population, the experimental units (e.g., marked animals) are independent, observation periods are independent, working radios are always located, right-censoring is random, and that radios do not impact survival (Winterstein et al. 2001). Right-censoring occurs when an individual “leaves” a study either temporarily or permanently and the fate of the individual is unknown.

I must assume that captured females were a random subset of the population as all captured females were marked. This assumption holds if nearly all females attend leks in the spring for breeding. Males were marked so that an equal number from each lek were monitored. To reduce bias in sampling, all leks were trapped on our study areas over a relatively short period. Birds were tracked daily to enhance the detection probability of functioning radios and transmitters with a mortality pulse (detection distance was ~1.6

km). Although an individual may have been missed for a day or so, birds that had not permanently emigrated were found within a weekly sampling period. I modeled survival with time units ≥ 1 week as these were more likely to be independent given that I estimated survival over 9- and 12-month periods. Month was the base time unit for the 12-month estimates as aerial surveying was conducted monthly from September 2002 through March 2003. Birds were right-censored from the encounter histories if they were known to emigrate or if a radio signal was lost. A 2-year comparison of survival rates of radiomarked and banded birds from our study area found no measurable effect of radiomarking (Chapter 2). I used a staggered entry known-fate encounter history and included individuals after a 2-week acclimation (Winterstein et al. 2001) to the radio-collar. Most birds would have entered the encounter history once our trapping efforts had ceased. In fact, most mortality that occurred during the trapping season was excluded from the analysis.

I estimated survival rates using known-fate models in MARK 3.0 (White and Burnham 1999). Models were developed using the design matrix feature and a logit link function. Global models were the most highly parameterized model, but not necessarily saturated models. Model goodness-of-fit was evaluated by examining residual plots. Model selection was based on the minimization of Akaike's Information Criterion corrected for small samples sizes (AIC_c), and AIC_c weights (w_i 's) to select the model best supported by the data. I used multi-model inference and model averaging in cases where the difference in AIC_c values (ΔAIC_c) between the best and subsequent models was < 2 (Burnham and Anderson 1998). Model averaging was used to refine parameter estimates from candidate sets with several competing models. In this procedure, parameter

estimates (i.e., survival and standard errors) are calculated as a weighted mean using AIC_c weights.

Data sets and candidate models

Transmitters in this study had different expected battery life; those used from spring 1997 through fall 1999 had maximum life of 6 to 9-months (hereafter summer), and those used from 2000 to 2003 had approximately a 12-month maximum life (hereafter seasonal) (Table 1). I used the summer data to increase sample size of cohorts across years (Table 1). However, these data may be biased if used to extrapolate to 12-month survival estimates as they exclude winter survival. The bias could be positive if winter survival is appreciably greater than the previous 8 months. Therefore, I analyzed the seasonal data as a verification of the results from the summer analyses. In both sets of analyses, data were pooled across various cohorts (Table 1) in order to have sufficient sample sizes ($n \geq 25$) to detect differences in timing and overall survival rates across groups (Winterstein et al. 2001). Admittedly, such pooling may weaken the power of the analyses, as there could have been confounding factors.

RESULTS

In total, 781 lesser prairie-chickens were captured during the 6-year study. Of these, 136 males (46 yearling, 66 adult, 24 age undetermined) and 227 females (87 yearling, 117 adult, and 23 age undetermined) were fitted with radio-transmitters (Table 1). Fifteen birds (4%) (8 males and 7 females) died within the 2-week adjustment period after marking. Birds were right-censored (30.8 %; 112 of 363 radiomarked individuals) because of collar slippage and radio failure (79.5 %; 89 of 112), and emigration (20.5 %; 23 of 112) to other sagebrush fragments.

Summer survival

Monthly variation in survival was an important structure to all candidate sets, as either an additive or a main effect (Table 2). Much of the time dependent variation was centered on the nesting season (Fig. 1). Yearly variation in female summer survival was well supported by the data ($w_i = 0.60$), as summer survival (\hat{S}) varied from 0.537 to 0.866 between 1997 and 2002 (Table 3). Age-specific survival of females with an additive monthly effect (Fig. 1) was reasonably well supported by the data ($w_i = 0.54$); however, monthly variation alone fit nearly as well ($\Delta AIC_c = 0.74$; $w_i = 0.38$) (Table 2). Yearling females survived at a slightly higher rate ($\hat{S} = 0.757$, SE = 0.041) than adult females ($\hat{S} = 0.692$, SE = 0.041) during the summer (Table 3). Overall the monthly timing of mortality (Fig. 2) and survivorship for males ($\hat{S} = 0.692$, SE = 0.050) and females ($\hat{S} = 0.666$, SE = 0.053) were similar, as time dependent and constant survival models fit better than those with gender effects. There were several competing models in this candidate set, as the top 5 models all had $\Delta AIC_c < 2$ and w_i 's ranging from 0.13 to 0.29 (Table 2). However, a plot of biweekly survival for each gender (Fig. 2) indicated that female survivorship was inversely related to the cumulative number of females incubating nests, and increased as nesting activities ceased. Alternatively, male survivorship appeared to decrease periodically during the breeding season (Fig. 2).

Seasonal survival

Monthly variation was also important in model selection of the seasonal data, as month was in the top 2 models of each candidate set (Table 4). Gender- and time-specific survival was the most parsimonious model; however, the timing of mortality may have been more important (Fig. 3) as the probability for males ($\hat{S} = 0.39$ SE = 0.10) to

survive 12-months was similar to that of females ($\hat{S} = 0.43$ SE = 0.05) (Table 5). Age-specific survival with an additive time effect for females was well supported; however, monthly variation alone was a highly comparable model ($w_1/w_2 = 1.2$; Table 4). The probability of yearling females surviving the interval was substantially higher ($\hat{S} = 0.52$ SE = 0.08), than that of adults ($\hat{S} = 0.37$ SE = 0.06), but the difference in these probabilities estimated from model averaging was less than non-averaged estimates ($\hat{S}_{\text{yearling}} = 0.48$ SE = 0.06; $\hat{S}_{\text{adult}} = 0.40$ SE = 0.05)(Table 5). Monthly variation in survival (Fig. 3) indicated that the greatest mortality occurred during the reproductive season (\hat{S} for Apr – Jul = 0.69, SE = 0.04), but winter survival (Nov – Feb) was not much higher ($\hat{S} = 0.77$, SE = 0.06).

Probable causes of mortality

One-hundred and thirty four mortalities were recorded from spring 1997 to spring 2003 (Table 6). The majority of mortality was attributed to mammalian predation (54%). It is likely that coyotes were the primary mammalian predator, as most sign at recovery locations suggested canid predation. Five whole carcasses were cached under shrubs, but could only be classified as mammalian predation. Most of the mammalian predation (75%) was associated with female mortality ($G^2 = 4.96$, df=1, $P = 0.004$) and coincided with losses during nesting (>30%).

Raptor predation occurred primarily during spring and winter, which coincided with presence of wintering or migratory populations of red-tailed hawk (*Buteo jamaicensis*), ferruginous hawk (*Buteo regalis*), rough-legged hawk (*Buteo lagopus*), northern harrier (*Circus cyaneus*), and a few prairie falcons (*Falco mexicanus*). Great-horned owls (*Bubo virginianus*) were present year round and were probable predators;

however, with no raptor predation in summer it is thought that their role as a predator was minimal. Males seemed more susceptible to raptor predation (20%) than females (11%), but this rate was not measurably different ($G^2 = 1.88$, $df=1$, $P = 0.170$). Seven of the 8 accidents were associated with powerline collisions, and one female was killed by farm machinery while incubating a nest in an alfalfa field. Snakes were responsible for the mortalities of 3 nesting females. These females were > 20 days into incubation when they were killed, and were likely tenacious in defending the nest. The gopher snake (*Pituophis catenifer*) was the probable predator as this species was observed depredating the eggs at 4 nests, and is the only snake on the study area large enough to constrict and attempt to swallow the head and neck of a female. Losses to recreational hunting were small (5%) relative to the radiotelemetry population, but even less (1.2% of 655 birds) when compared to banded birds ($781[\text{total banded}] - 126[\text{known mortalities}] = 655$) that were available for harvesting. Males apparently were more susceptible (15%; 7 of 44) to hunting losses than females (1%; 1 of 90) ($G^2 = 8.74$, $df=1$, $P = 0.003$)

DISCUSSION

Yearly variation in summer survival was evident and seemed to be highly related to mortality rates of incubating females on nests (Fig. 1); >30% of all female mortality was associated with the nesting period. Summer survival rates and apparent nest success (number of nests hatching >1 egg / total number of nests) from 5 years revealed the strength of this relationship (Fig. 4). Changes in predator communities and/or residual cover may have influenced nest success and/or female losses (Bergerud 1988), but such factors were not measured in this study. However, management efforts that would increase nesting success may markedly increase annual female survival.

Gender-specific survival

Gender-specific survival was not well supported by the data, as the overall survival rates of males and females were similar in the summer and seasonal analyses. However, the timing of survival over 12 months suggested that seasonal patterns in male survivorship do not match the temporal pattern seen in females. The conspicuous displays (or its physiological costs) of males may increase their vulnerability in both spring and fall thereby equalizing the female losses during nesting (Amman 1957). This result contradicts Bergerud's (1988) prediction that uniparental care will result in greater mortality in females than males.

If sexually selected characters increase mating success (e.g., conspicuous plumage or behavior), then characters that increase survival (e.g., cryptic plumage or behavior) should make a relatively small contribution to total fitness (Angelstam 1984). In grouse, this should result in a lower survival rate in males (the gender with sexually selected traits in this case) than females. One might expect this pattern to be evident in the most sexually dimorphic species, capercaillie (*Tetrao urogallus*), greater sage-grouse (*Centrocercus urophasianus*), blue grouse (*Dendragapus obscurus*), and black grouse (*Tetrao tetrix*). Several studies have examined annual survival rates in male and female grouse and the results have been mixed. Greater sage-grouse are the only species in this group in which males have lower survival rates than females (Zablan et al. 2003). Less sexually dimorphic species, white-tailed ptarmigan (*Lagopus leucurus*) and spruce grouse (*Falcapennis falcapennis*) also exhibit gender-specific patterns of survival (Choate 1963, Braun 1969, Ellison 1974, Keppie 1979), but the white-tailed ptarmigan are socially

monogamous. However, capercaillie exhibit the inverse with males having markedly higher survival in 4 regions of Europe (Storch 2001), and male black grouse survival is \geq to that of females (Angelstam 1984, Caizergues and Ellison 1997). Survival rates of male blue grouse, greater prairie-chicken (*Tympanuchus cupido*), sharp-tailed grouse (*Tympanuchus phasianellus*), lesser prairie-chicken, hazel grouse (*Bonasa bonasia*), ruffed grouse (*Bonasa umbellus*), and rock ptarmigan (*Lagopus lagopus*) are nearly equal to those of females (Weeden 1965, Elliot and Bendell 1967, Gullion and Marshall 1968, Hamerstrom and Hamerstrom 1973, this study).

The lack of a consistent pattern across studies makes it difficult to draw conclusions about the role or presence of gender-specific survival rates, and to account for markedly different investments in breeding strategies between males and females (Bergerud 1988). The relatively equal survival rates of male and female lesser prairie-chickens suggest that the cost of reproduction has balanced female losses during nesting with male mortality during display and at other times of year. Alternatively, the similar plumages between males and females may equalize the survival rates when males are not displaying. Additionally, these comparable survival rates contradict the idea that male biased sex-ratios are a result of differential survival (Amman 1957, Campbell 1972, Moss 1987, Linden 1981, Bergerud 1988), suggesting that such ratios may reflect a bias for males to be susceptible to hunter harvest. While speculative, this conclusion is supported by the fact that 7 of 8 hunter harvested birds in this study were males. Taylor and Guthery (1980) documented that male lesser prairie-chickens visited grain fields in flocks, and females did so in singles. Because the common method of hunting prairie

chickens involves pass-shooting flocks coming into grain fields, there is some support for this claim.

Age-specific survival

Age-specific patterns in female survival were evident in both analyses with yearling birds surviving at a higher rate than adults. This was surprising given that yearlings of other grouse species tend to have reduced survival and reproductive output (Bergerud 1988, Saether 1990). However, the timing of mortality was consistent between these groups as models with an additive time effect ($S_{\text{age} + \text{month}}$) were the most parsimonious in both sets of analyses, with the lowest survival rates during the nesting and brooding periods. One might predict that the cost of reproduction would result in reduced survival rates of adults, if they had higher reproductive output. However, reproductive parameters were similar between age-classes in this study (Fig. 5), except that yearling nest success, 33% (SE = 5 %), was marginally higher than adults, 28% (SE = 4%). Whereas rates of nest loss were comparable, mortality rates were not. The reason for such differences suggests different responses to depredation events on adults and yearlings. Adult females may have been more tenacious (i.e., a fight response) in nest guarding (see Hannon and Smith 1987), whereas the yearlings may have had a flight response to nest predators. If true, this could explain the lower survival rate for adult females.

Probable causes of mortality

Predator classification from evidence at kill sites may be problematic, because mammalian scavengers may be most abundant in a region (Bumann and Stauffer 2002). Overestimation of mammalian-kills increases as a function of ambient temperature, and

could have occurred in this study. However, if a positive bias occurred in this study it is likely that it was consistent for both males and females. Thus, the magnitude of the difference in cause specific mortality rates should be a reasonable index to compare proportional losses between males and females.

The probable causes of mortality lesser prairie-chickens differed somewhat between males and females, as 60% of predation on females was classified as mammalian, 1.5 times as much as males (40%). Conversely, male losses (20%) were classified as raptor predation more so than females (11%). This potential difference is likely from the types of predators cueing on breeding and nesting behaviors of males and females, respectively. Northern harriers have been documented harassing and killing prairie grouse (Berger et al. 1963, Toland 1985, Haukos and Broda 1989). The susceptibility of males to mortality may not occur at the lek site (Berger et al. 1963), but the physiological cost of display (Vehrencamp et al. 1989) may increase the probability of predation both during and after breeding season (Angelstam 1984). Mammalian predation of displaying birds is probably rare (Hamerstrom et al. 1965), and this pattern was likely true in my study. Spring and fall raptor migrations coincided with display activities of lesser prairie-chickens in this study, thus likely increasing their susceptibility to raptor predation.

In 2001, 2 females died of unknown causes during the nesting season. Each carcass was recovered intact and with a brood patch (i.e., an area of the ventral surface of the abdomen that a female will pluck to line the nest with feathers). One hen had been incubating for 12 days at the date of death. The other had not been located on a nest although her radiolocations suggested she had been laying eggs for ≥ 8 days. These birds

were submitted for necropsy at the Diagnostic Laboratory, Kansas State University, College of Veterinary of Medicine. Avian cholera (*Pasturella multlicoda*), was isolated from various tissues of 1 female, and was suggested to be the cause of death.

Accidental death due to powerline and/or fence collisions has a substantial impact on populations of European grouse (Miquet 1990, Bevanger 1995, Moss et al. 2000). Powerline collisions occurred as birds were leaving the prairie to forage in adjacent agricultural fields. This loss appeared to be relatively small in my study population, accounting for 5% of all mortality, similar to rates estimated for greater sage-grouse in Idaho (Connelly et al. 2000). It is possible that some portion of the “unknown” category was associated with powerline collisions, thus 5% may be a conservative estimate. Powerline densities were relatively low on the study area as they usually traversed a partial length of the prairie edge (< 40 % of 100 km of edge).

Hunting mortality was low in this study of radiomarked birds ($\leq 5\%$) and even less for all birds (<1.5 %). Research on European grouse suggests that hunting mortality of <10% should not impact spring breeding populations (Ellison et al. 1988, Ellison 1991a, b). Ellison (1991a) suggested that even declining populations can sustain some harvest (~5%) without negatively impacting production. Alternatively, Small et al. (1991) found that hunting mortality of 20% was mostly additive to both adult and juvenile ruffed grouse. Connelly et al. (2000) suggested that harvest of females was additive to over-winter mortality, but that some level of exploitation (~10 %) was tolerable given the high annual variability in hunter success. Recreational hunting losses appeared to have minimal impact on the study population in reducing either annual survival or numbers of breeding birds in the spring.

MANAGEMENT IMPLICATIONS

Management of lesser prairie-chickens should focus on habitat manipulations that increase nest survival and decrease female losses during incubation. In fragmented populations, predator control may achieve short-term goals of increased female survival and nest success, but may be too costly to sustain in the long-term (Schroeder and Baydack 2001). Long-term management should focus on creating nesting habitat that decreases losses to mammalian predation. Similarly, experimental work is needed to understand the mechanisms by which mammalian predators search and find nests. Specifically identifying habitat structure that lowers the success of nest predators on nests and on females would be most advantageous for long-term habitat management. Limiting harvest probably would have little impact on the lesser prairie-chickens in Kansas since most mortality occurs during the nesting season. However, more accurate information is needed on harvest rates throughout lesser prairie-chicken range. Current harvest levels are estimated indirectly through mail surveys to upland gamebird hunters, who may not actually hunt prairie chickens. A free permit system specific to prairie chicken hunters would facilitate a direct measure of hunter harvests.

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Table 1. Numbers of yearling (Y) and adult (A) lesser prairie-chickens radiomarked in Finney County, Kansas 1997-2002.

Year	Males			Females				
	Area I <i>n</i> (Y,A)	Months ^a	Area II <i>n</i> (Y,A)	Months	Area I <i>n</i> (Y,A)	Area II <i>n</i> (Y,A)	Months	
1997-1998	24 (no-age) ^b	9	ND ^c	ND	23 (no-age) ^{b,d}	ND	9	ND
1998-1999	34 (17, 17) ^b	12 ^h	ND	ND	23 (18, 5) ^{b,d,e}	ND	9	ND
1999-2000	41(18, 23) ^b	12 ^h	ND	ND	34 (18, 16) ^{b,d,e}	ND	9	ND
2000-2001	ND	ND	12 (5, 7) ^g	12	26 (7, 19) ^{d,e,f,g}	25 (11, 14) ^{e,f,g}	12	12
2001-2002	2(0, 2) ^g	12	13 (6, 7) ^g	12	33 (12, 21) ^{d,e,f,g}	23 (8, 15) ^{e,f,g}	12	12
2002-2003	ND	ND	ND	ND	14 (3, 11) ^{d,e,f,g}	26 (10, 16) ^{e,f,g}	12	12
Totals	101(35, 42)	ND	25 (11, 14)	ND	153 (58, 72)	76 (29, 45)	ND	ND

^a Maximum battery life and tracking period in months for a given cohort.

^b Cohorts used to examine sex-specific rates for 9 month period; ages and years pooled.

^c ND = no data available.

^d Cohorts used to examine annual variation in survival rates for 9 month period; ages pooled.

^e Cohorts used to examine age-specific rates in females for 9 month period; areas and years pooled.

^f Cohorts used to examine age-specific rates in females for 12 month period; areas and years pooled.

^g Cohorts used to examine sex-specific rates for 12 month period; ages, areas, and years pooled.

^h Twelve months of coverage was possible due to fall trapping efforts.

Table 2. Candidate models and model statistics for summer survival (Apr-Nov) of lesser prairie-chickens in Finney County, Kansas, 1997-2002.

Model structure	Model statistics ^a				
	AIC _c	ΔAIC _c	w_i	K	Dev
Annual variation (females only)					
$S_{\text{year} + \text{month}}$	370.02	0.00	0.60	14	60.75
$S_{\text{year} + \text{biweek}}$	372.11	2.09	0.21	23	44.38
S_{month}	372.30	2.28	0.19	9	73.20
S_{constant}	399.08	29.06	0.00	1	116.09
S_{year}	399.10	29.09	0.00	6	106.06
Age-specific (females only)					
$S_{\text{age} + \text{month}}$	454.86	0.00	0.55	10	21.43
S_{month}	455.60	0.74	0.38	9	24.19
$S_{\text{age} + \text{biweek}}$	459.85	4.99	0.05	19	8.17
S_{biweek}	460.44	5.58	0.03	18	10.79
$S_{\text{age} * \text{month}}$	468.51	13.66	0.00	18	18.87
Gender-specific					
S_{month}	353.01	0.00	0.29	9	38.97
S_{constant}	353.65	0.65	0.21	1	55.72
S_{biweek}	354.36	1.35	0.15	18	22.00
$S_{\text{sex} + \text{month}}$	354.45	1.45	0.14	10	38.39
S_{sex}	354.67	1.67	0.13	2	54.74
$S_{\text{sex} + \text{biweek}}$	355.81	2.81	0.07	19	21.41
$S_{\text{sex} * \text{month}}$	358.68	5.68	0.02	18	26.32

^a Model fit is described with deviance (Dev), the number of parameters (K), and Akaike's Information Criterion corrected for small sample size (AIC_c).

Table 3. Summer survival estimates for radiomarked lesser prairie-chickens after marking (Apr – Nov) 1997-2002.

Group	Parameter estimates		
	\hat{S}	SE	95% CI
Year (females only)			
1997	0.556	0.110	0.340, 0.772
1998	0.845	0.083	0.683, 1.000
1999	0.777	0.081	0.619, 0.935
2000	0.537	0.102	0.337, 0.737
2001	0.548	0.092	0.368, 0.729
2002	0.866	0.088	0.694, 1.000
Age-specific (females only)			
Yearling	0.757	0.041	0.677, 0.836
Adult	0.692	0.041	0.612, 0.773
Gender-specific			
Male	0.692	0.050	0.594, 0.790
Female	0.666	0.053	0.562, 0.771

Table 4. Candidate models and model statistics for seasonal (Apr-Mar) survival of lesser prairie-chickens in Finney County, Kansas, 2000-2003.

Model structure ^b	AIC _c	ΔAIC _c	w_i	K	Dev
Gender-specific					
$S_{\text{sex} * \text{month}}$	543.72	0.00	0.61	24	17.16
S_{month}	545.24	1.52	0.28	12	43.53
$S_{\text{sex} + \text{month}}$	547.15	3.43	0.11	13	43.39
S_{constant}	556.34	12.62	0.00	1	76.92
S_{sex}	558.19	14.47	0.00	2	76.76
Age-specific (females only)					
$S_{\text{age} + \text{month}}$	455.91	0.00	0.55	13	429.51
S_{month}	456.32	0.41	0.45	12	431.97
$S_{\text{age} * \text{month}}$	470.49	14.59	0.00	24	421.16
S_{age}	471.51	15.61	0.00	2	467.50
S_{constant}	472.39	16.47	0.00	1	470.37

^a Model fit is described with deviance (Dev), the number of parameters (K), and Akaike's Information Criterion corrected for small sample size (AIC_c).

Table 5. Seasonal survival estimates for radiomarked lesser prairie-chickens
12-months after marking (Apr – Mar) 2000-2003.

Group	Parameter estimates		
	\hat{S}	SE(\hat{S})	95 % CI
Gender-specific ^a			
Male	0.393	0.100	0.175, 0.630
Female	0.432	0.050	0.335, 0.533
Age-specific (females only) ^a			
Yearling	0.481	0.066	0.379, 0.673
Adult	0.400	0.054	0.272, 0.504

^a Parameter estimates were derived using the model averaging
procedure in MARK.

Table 6. Numbers and percentages of potential mortality causes of lesser prairie-chickens in Finney County, Kansas, 1997 – 2003.

Potential cause	1997-1999			2000-2003			1997-2003
	Female ^a	Male	Total	Female ^a	Male	Total	Overall ^a
Mammal	15	10	25 (61%)	39	8	47 (51%)	72 (54%)
Unknown	2	3	5 (12%)	17	4	20 (22%)	25 (18%)
Raptor	1	4	5 (12%)	9	5	14 (15%)	19 (14%)
Accident	1	1	2 (5%)	3	3	6 (6%)	8 (6%)
Hunter ^b	0	4	4 (10%)	1	2	3 (3%)	7 (5%)
Snake	0	0	0	3	0	3 (3%)	3 (2%)
Total	19	22	41	71	22	93	134

^a Mortality during nesting was a considerable portion (32%) of all female losses 10 of 22 (46%) and 19 of 68 (27%) during 1997-1999, and 2000-2003, respectively.

^b Harvest rates are biased high as reported birds were banded only, and not radiomarked.

Fig. 1. Annual variation in monthly survival rates (9-months) of females (A) from the model $S_{\text{year} + \text{month}}$, standard errors not included for clarity. Yearling and adult female survival rates (B) from the model $S_{\text{year} + \text{month}}$. Male and female survival (C) from the model $S_{\text{gender} * \text{month}}$ (1997-1999).

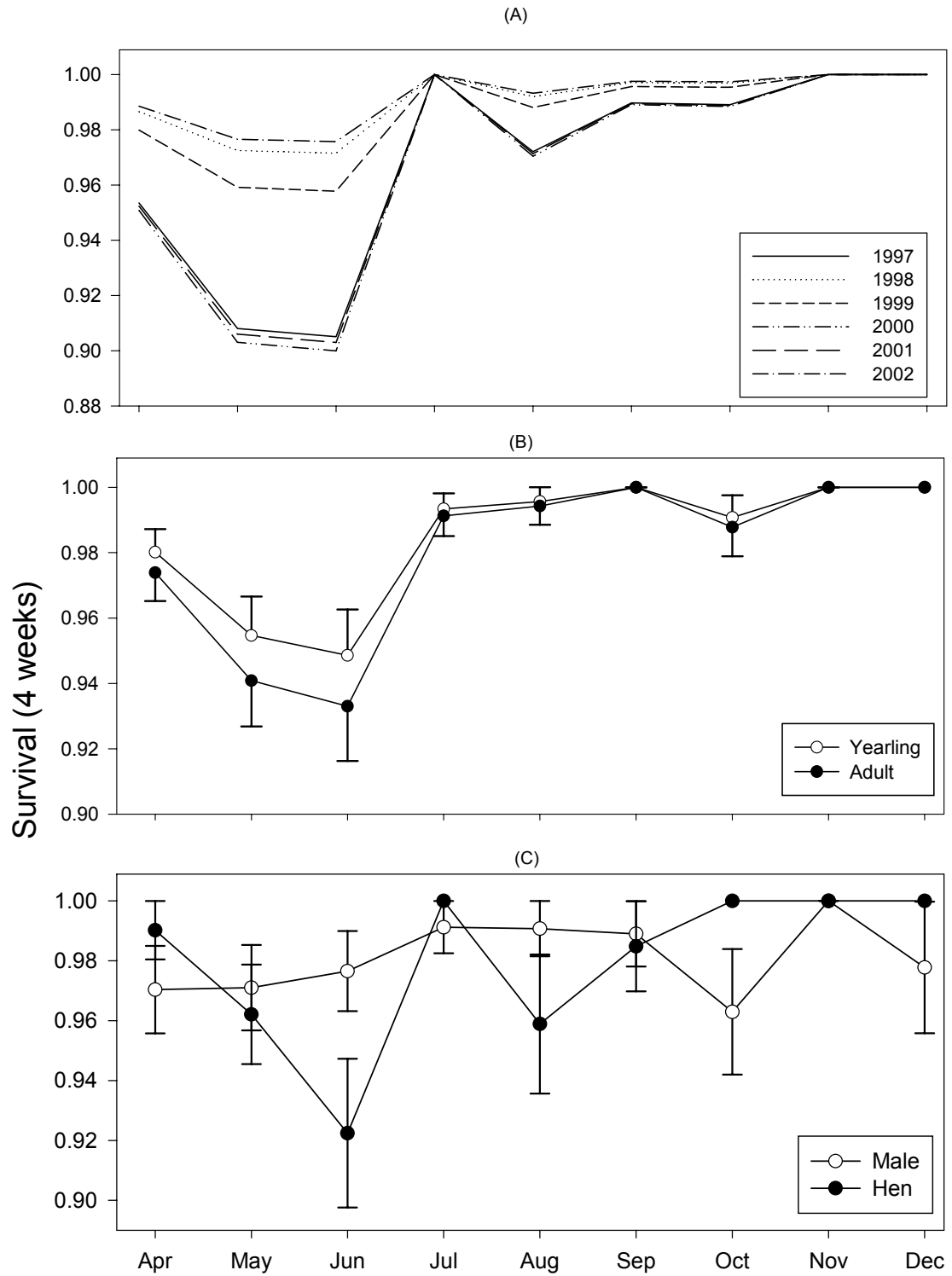


Fig. 2. Relationship between biweekly survival rates of males (dashed line) and females (solid line) and the cumulative frequency distribution (CFD) of incubating females (gray). Note the inverse relationship of female survival relative to the CFD of nests.

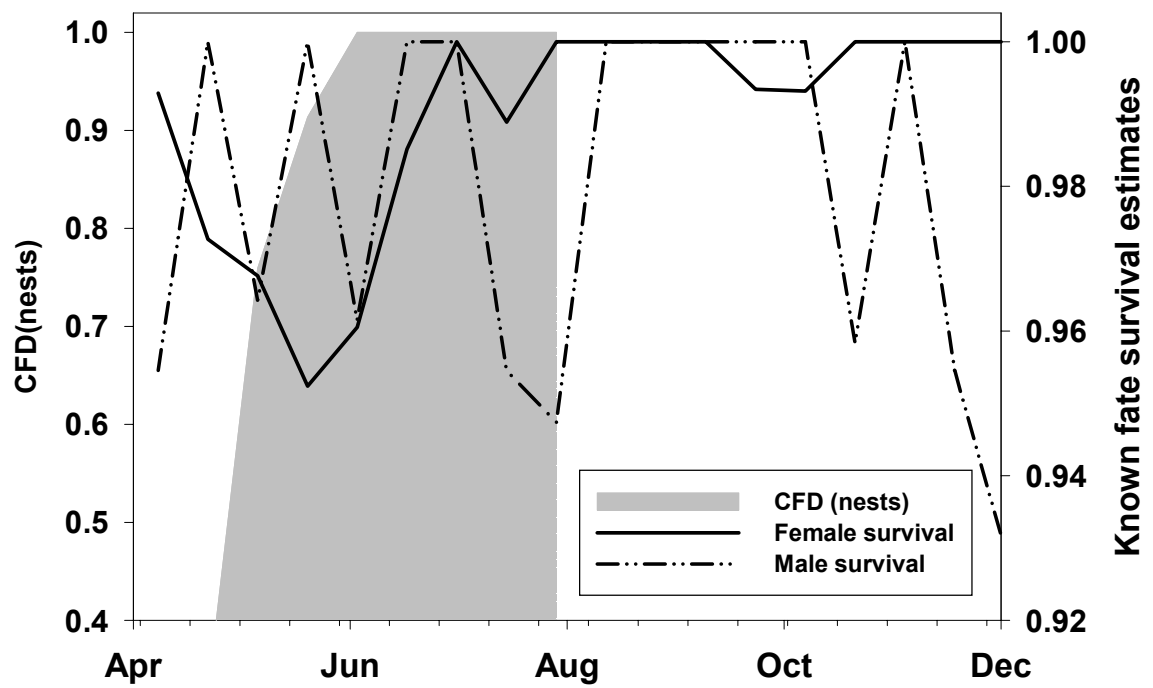


Fig. 3. Monthly survival rates of males and females (A) for 12-months (2000-2003) from the model $S_{\text{gender*month}}$. Note the variation in the timing of survival between the groups. Monthly survival rates for yearlings and adults (B) for 12-months.

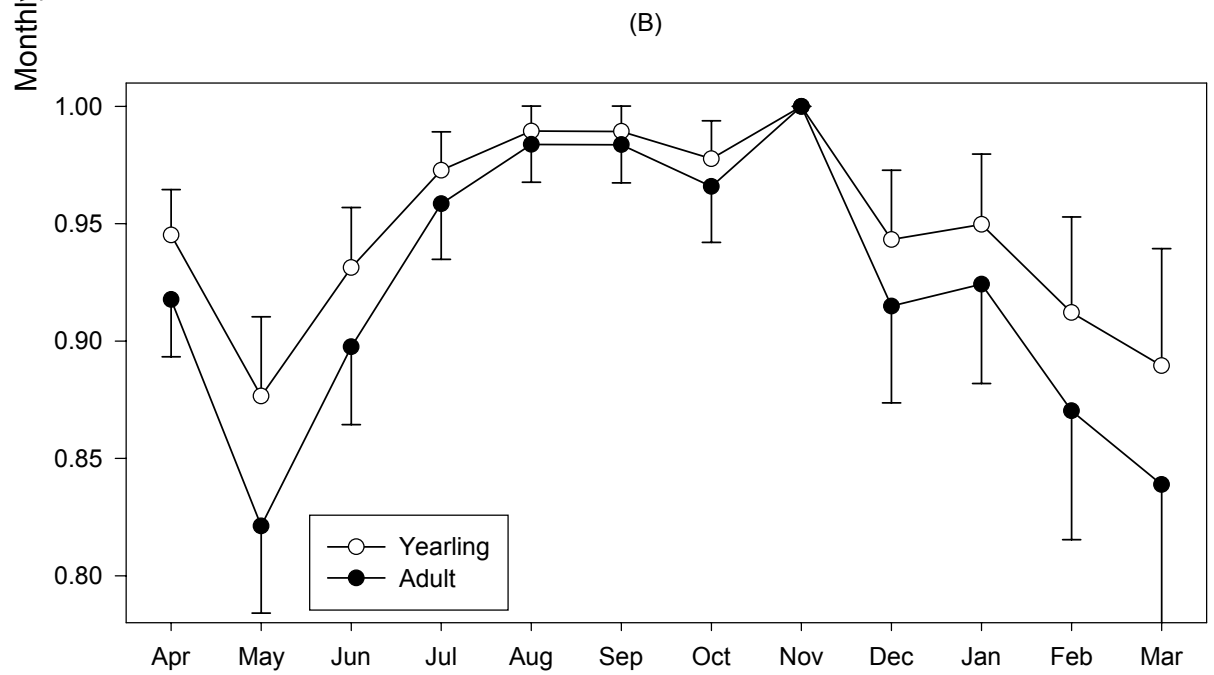
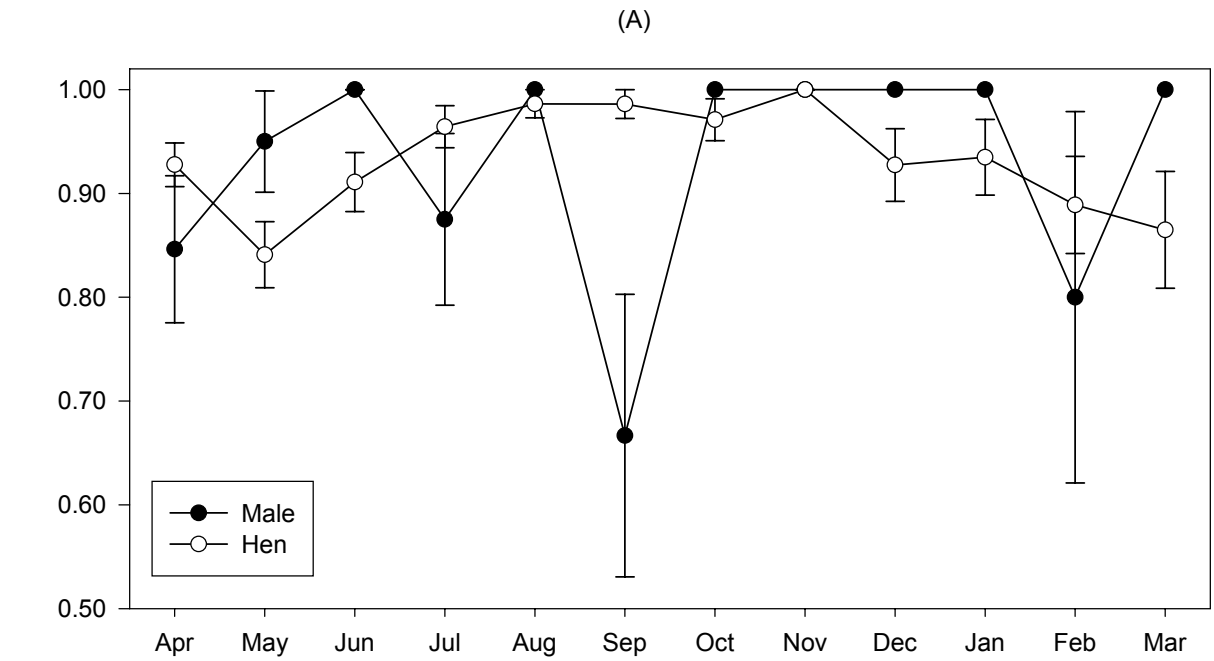


Fig. 4. Nest success (black) and female survival (white) \pm SEs for 1998-2002. Nests from 1997 were not included due to different nest marking techniques.

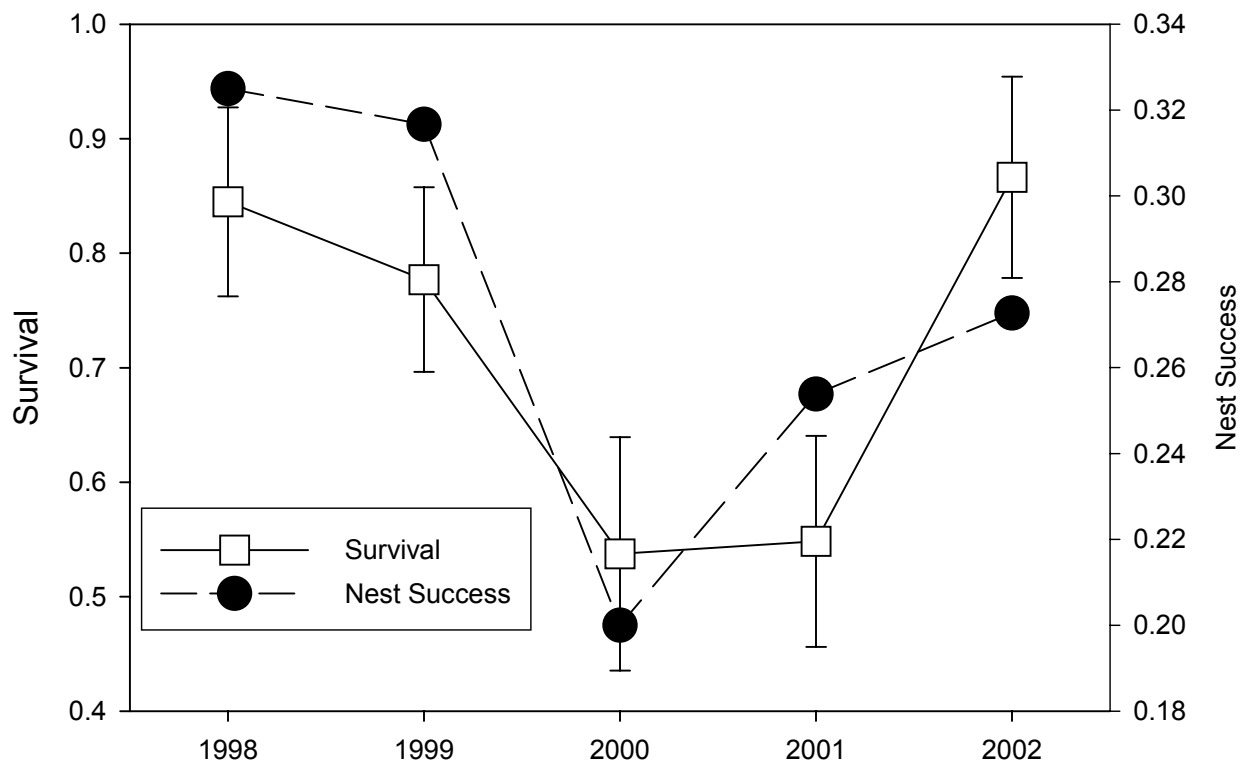
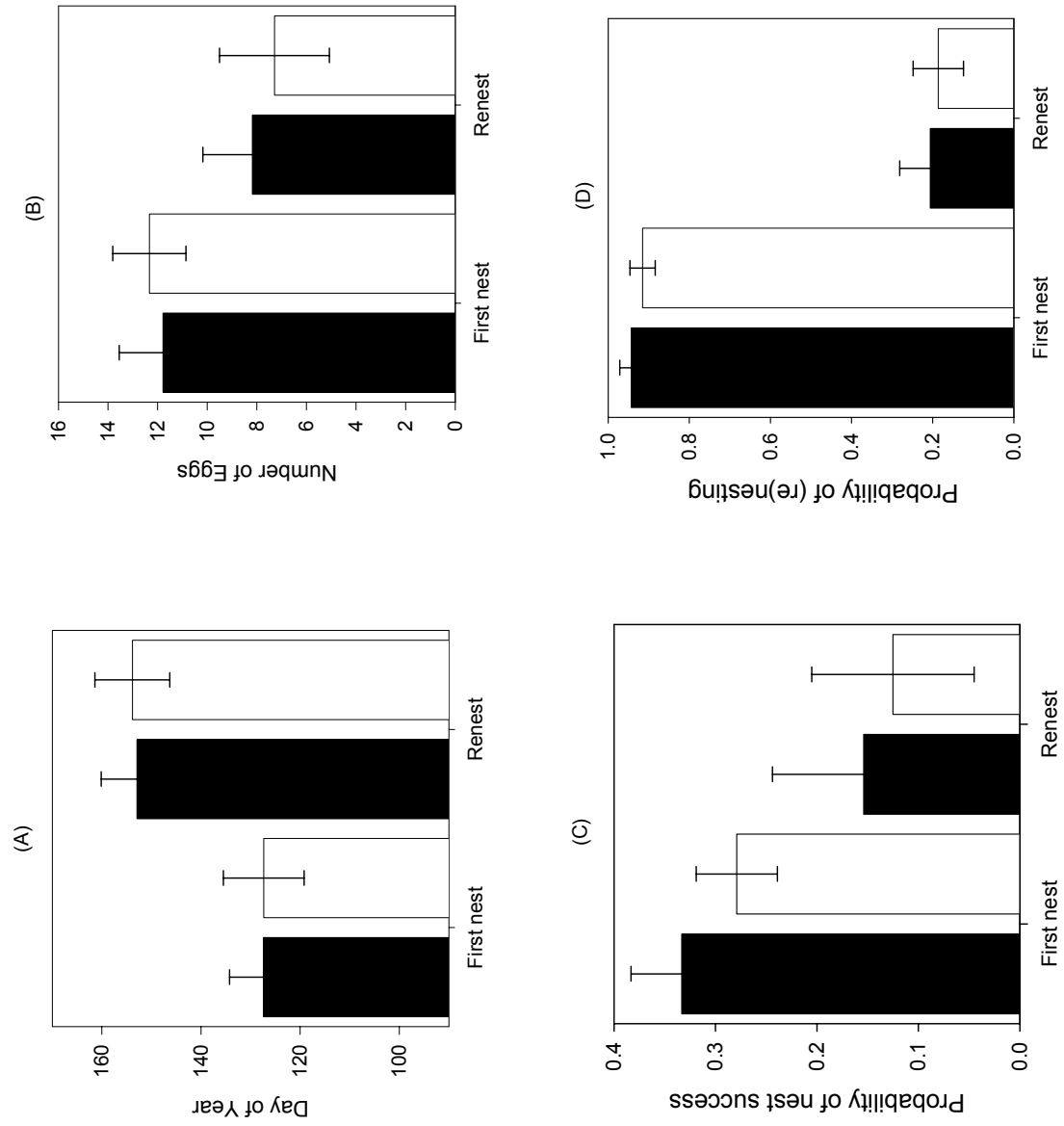


Fig. 5. Reproductive parameters of female lesser prairie-chickens (black =yearling; white = adult) from 1998 to 2002. Note the consistency among clutch size, incubation date, and probability of (re)nesting (A, B, and D) with only slight separation in nesting success (C) between the age-classes.



CHAPTER 4

LESSER PRAIRIE-CHICKEN DEMOGRAPHY: A SENSITIVITY ANALYSIS OF POPULATION DYNAMICS IN TWO PRAIRIE FRAGMENTS

Abstract. Recently it has been suggested that nest success and chick survival are the main limiting factors for populations of lesser prairie-chicken (*Tympanuchus pallidicinctus*) in the sand sagebrush (*Artemisia filifolia*) prairie of southwestern Kansas. This hypothesis was examined using elasticity analysis on an age-specific projection matrix. The model was parameterized with demographic data from a 1998 to 2003 field study of radiomarked lesser prairie-chickens near Garden City, Kansas. Additionally, the projection matrices of two spatially implicit populations were compared to examine the contributions of the vital rates to the difference in the rate of population change (λ) between these fragments with contrasting human disturbance and sand sagebrush communities. Lambda was less than 1.0 for both populations ($\lambda^I = 0.544$, $\lambda^{II} = 0.754$). This indicated a decline in population growth in the absence of immigration. However, the marked contrast in the contributions to λ between populations yielded differences in sensitivity to various life-stages, and prescribed management practices on the two areas. The application of this analysis to management of the sand sagebrush habitat could possibly increase the effectiveness of management efforts.

INTRODUCTION

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is one of five prairie grouse species that requires native grasslands and shrublands for breeding, nesting, and annual survival. Historically this species' range was one of the most limited, concentrated in the mixed- and short-grass sand sagebrush (*Artemisia filifolia*) and sand shinnery oak (*Quercus havardii*) prairies of southeastern Colorado, eastern New Mexico, the panhandle of Texas, western Oklahoma, and southwestern Kansas (Giesen 1998). This historic range has been further reduced and fragmented due to dry land agriculture and more recently mechanized irrigation (Waddell and Hanzlick 1978). It is estimated that over 90% of the range has been lost since the turn of the 20th century (Giesen 1998) and the range-wide population decline has paralleled these losses. In 1995, the lesser prairie-chicken was petitioned to be listed as threatened under the Endangered Species Act (Giesen 1998). The U.S. Fish and Wildlife Service (USFWS) determined that such a listing was "warranted but precluded" and this status is reviewed annually (USFWS 2002). Because of recent population declines, sport-hunting seasons were closed in New Mexico in 1996 and in Oklahoma in 1998. Currently, a 2-day hunting season and 2/4 bird bag/possession limit occur in Texas, and Kansas has a 2-month hunting season and 1/4 bird bag/possession limit. Given the status of this sensitive species it is critical to understand the dynamics of local and regional populations and identify possible management scenarios that would most effectively benefit the lesser prairie-chicken.

An important concern for wildlife managers working with sensitive species is knowing what constrains the population or which management practices will have the greatest impact on the population (Peterson et al. 1998). Given the short duration of

research budgets it is often necessary to provide an adaptive framework for which populations can be managed with short-term management experiments. That is, develop a management hypothesis, implement the program, and assess the results of a given experiment. Risk assessment models and population viability analyses (PVA) have been used to provide insight to the management of sensitive wildlife species (Crouse et al. 1987, Wisdom and Mills 1997, Johnson and Braun 1999, Blakesly et al. 2001). Similar approaches have been used in providing conservation guidelines for other grouse species, including the two subspecies of the greater prairie-chicken (*T. cupido pinnatus*; Wisdom and Mills 1997: and *T. c. attwaterii*; Peterson et al. 1998), sharp-tailed grouse (*T. phasianellus*; Temple 1992), greater sage-grouse (*Centrocercus urophasianus*; Johnson and Braun 1999), black grouse (*Tetrao tetrix*; Caizergues and Ellison 1997), capercaillie (*Tetrao urogallus*; Grimm and Storch 2000), and willow ptarmigan (*Lagopus lagopus*; Steen and Erikstad 1996). Generally, these analyses have concluded that recruitment was the limiting factor affecting growth of populations with low adult survivorship. This follows Bergerud's (1988) hypothesis that nesting and brood rearing are the limiting factors for grouse. Studies of longer lived species found that hunting mortality may have been additive in years of poor recruitment (Steen and Erikstad 1996, Caizergues and Ellison 1997, Johnson and Braun 1999). Few models were based on an ecological study, and most required the use of surrogate parameter estimates from a closely related species, age- or sex-ratios from harvest data, or previous publications of the study species.

This paper describes the development of an age-based matrix model of lesser prairie-chicken population dynamics that compares the relative importance of the reproductive and survival rates in two spatially implicit populations. The analyses in this

paper were based on a comprehensive ecological study from which vital rates were estimated for each life history stage. I followed the modeling framework of Caswell (2001) to address the various conservation concerns for this species and conducted the following: 1) population assessment, 2) diagnosis, 3) prescription and 4) prognosis. I assessed the lesser prairie-chicken populations by estimating the arithmetic rate of population change (λ) and its respective confidence intervals to determine whether the populations were stable ($\lambda \approx 1.0$) or reflective of the long-term negative trend in these populations (Jamison 2000). Retrospective analysis (or a Life Table Response Experiment) was used to diagnose the probable causes of the population status. A combination of prospective (e.g., elasticity and variance scaled sensitivity) and retrospective (life-stage simulation analyses) techniques was used to prescribe management strategies that were aimed at improving population status. Finally, I returned to estimates of λ for both populations for the prognosis.

Less than 5% of radiomarked birds moved between these areas in a given year, but emigration to other patches was 20%; estimates of various population parameters indicated that area specific rates were warranted. Thus, I defined these two areas as populations. The two study areas in southwestern Kansas differ in terms of human disturbance, within-patch fragmentation, and density of sand sagebrush.

The specific objectives for each population were to 1) quantify the rate of population change and examine whether the populations were stable, 2) compare the relative importance of each vital rate to population status, i.e., test the nesting and brood rearing limiting factor hypothesis, 3) identify which rate or combinations of rates have

the greatest management priority, and 4) determine what is the long-term viability of these populations.

METHODS

Study Areas

The study region was comprised of two ~5,000 ha fragments of native sand sagebrush prairie near Garden City, Finney County, Kansas. Prior to the 1970s, these areas were a contiguous tract of sagebrush grassland (Waddell and Hanzlick 1978). The development of center-pivot irrigation systems led to the conversion of 150,00 ha of sand sagebrush to agricultural land. These areas were separated by ~20 km of center-pivot irrigated fields of corn, alfalfa, and wheat. Vegetation in the prairie fragments was primarily sand sagebrush, yucca (*Yucca* spp.), bluestem (*Andropogon* spp.), and big sandreed (*Calamovilfa gigantea*). Soils were in the choppy sands range site category, and topography was generally flat to rolling hills and dunes (Hullett et al. 1988). The native rangelands were grazed seasonally by livestock. Several of the pastures on both areas were treated with aerial applications of tebuthiron to control sagebrush densities.

These areas were similar in terms of overall type of habitat and land uses, but varied by the quantities of each (Table 1). However, Area I had more linear km of road (154 vs. 129 km), a higher density of pump-jacks (i.e., a device used in the extraction of natural gas or crude-oil) density (10.6 vs. 6.9 ha^{-1,000}), and more buildings (6 vs. 1; e.g., compressor stations, human dwellings) than Area II. Using the point-centered quarter method (Cottam and Curtis 1956), sagebrush density, height and diameter were estimated using 35 points (4 measurements per point) within a pasture (a discrete unit) and a weighted mean density (accounting for area [ha] of each pasture) was calculated across

pastures (Area I = 10 pastures, \bar{x} = 3,611, SE = 689; Area II = 15 pastures, \bar{x} = 4,206, SE = 697) for each area (Table 1) .

Field Procedures

Lesser prairie-chicken females were captured on leks during the spring (1998 to 2002) using walk-in funnel traps (Haukos et al. 1990). Each captured female was classified into an age-class yearling (≤ 10 mos) or adult (≥ 22 mos) by shape and wear on the outer primaries (Amman 1947, Copelin 1953), marked with an aluminum band on the tarsus, and fitted with a necklace-style lithium powered radio-transmitter with a mass < 12 -g. Transmitters were $\leq 1.9\%$ of a bird's body mass (\bar{x} = 783, range = 630-855 g) and below the recommended 3% level (Withey et al. 2001). Transmitters had either an 8- or 12-hour mortality switch, and 6-month (1998-1999) or 12-month (2000-2003) battery life. All radiomarked lesser prairie-chickens were tracked daily and remotely with a vehicle-mounted twin-Yagi null-peak telemetry system throughout the year to determine reproductive and survival status. Nesting data, brood size, and predation events of adults and post-fledgling chicks were determined from hand held telemetry systems.

The onset of incubation (± 2 days) was determined from radiotelemetry as females were localized for ~ 10 -day period and were found at the exact azimuths from fixed locations over a 3-day period. Nests were visited once at the onset of incubation to determine clutch size and once again later when the nest had either hatched or failed. If a female was absent from her nest for more than one day then the nest was visited on the second day to determine its fate.

Flush counts were used to estimate survivorship of broods to fledging, 34-days post-hatch. Thirty-four days was chosen as the fledging date because chicks

demonstrated the ability to survive separately from their natal brood for up to 2-weeks. Additionally chicks were first radiomarked at this age and known-fate survival was used to estimate survival beyond that date. Initial brood size was estimated from the number of hatched eggshells present in the nest. Broods were flushed at 14, 24 and 34-days post-hatch to determine changes in brood size over this period. These systematic flush counts were conducted at dawn when often the female was brooding the chicks.

Radiotelemetry was used to determine survival of chicks from fledging to first breeding and of breeding females. Thirty-four day old chicks (weighing ~ 200-g) were marked with a 2-g necklace style radio-transmitter with a 90-day battery life and were tracked daily. At 60-days post-hatch radiomarked chicks (weighing ~ 400-g) were recaptured and fitted with an adult size necklace style transmitters.

Demographic rates of lesser prairie-chickens

Clutch size (CLUTCH) was the total number of eggs laid in the nest (Table 2). Eggs were laid on the ground in a shallow scrape ~ 15 cm in diameter. Since all nests were found early in incubation the effects of partial clutch loss during laying would not have been detected. Partial clutch loss occurred in 30% of successful nests with a median of 2 eggs lost during incubation. Clutch sizes for both first and renests were used as constants for ages and areas, because biologically predicted to vary in this species (Giesen 1998), and practically there was little variation (Table 2).

Nest success (NEST) was estimated as apparent nest success, the proportion of nests hatching at least one egg. Mayfield estimates were not used because nests were found early in incubation and within 24-hrs of failure or hatch (Table 2). Rates of nesting success were estimated separately for each age and area.

Renesting (RENEST) was the probability of a female laying a replacement clutch, if her first nest failed. RENESE was calculated as the number of females laying renests divided by total number of unsuccessful first nests. Renests were detected and fates determined as described above. There were 5 cases in which the incubation date of a female's "first" nest was noticeably later (julian day > 143), than the mean (julian day = 127, SE = 8 days) for known first nests. In this case, it was assumed that these females lost their first clutch during laying and that the only nest documented for such an individual was a renest (Table 2). Small samples sizes precluded inputting these estimates as age specific rates.

Daily survival rates of pre-fledging chicks (CHICK) was estimated using a modified Mayfield estimator (Flint et al. 1995) applied to the change in brood size between flush counts. The daily rate was raised to the power of 34 to estimate survival over the 34-day period. This rate may be a conservative estimate if chicks were mixing with other broods (especially unmarked) at any time during the 34-day post-hatch period. Although, limited mixing (5%) was documented in radiomarked birds > 34 days of age in this study, mixing prior to this fledging period has not yet been documented in galliformes. Thus, the assumption was made that losses in brood size were deaths (Table 2). Small sample sizes precluded meaningful estimation between age-classes, but area specific rates were calculated.

I estimated survival rates of 34-day old chicks to first breeding (PBS, P_0) and annual survival rate for females (HEN, P_1 , P_2) using known-fate models in MARK 3.0 (White and Burnham 1999), and all models were developed using design matrices and logit link functions. Model fit was assessed by examining the residual plots. Model

selection was based on the minimization of Akaike's Information Criterion corrected for small samples sizes (AIC_c), and AIC_c weights (w_i 's) to select the model best supported by the data. Post-brood survival was estimated as one rate for all cohorts because of small sample sizes, but HEN survival was estimated for each cohort.

Population model

A deterministic female life-cycle model was constructed to summarize the age-structured variation in vital rates for both populations (Fig. 1). In this pre-breeding birth-pulse model, census occurred in April when birds were captured. The expected number of female chicks produced per female (F_i) were

$$F_i = [(\text{CLUTCH}_1 \times \text{NEST}_1) + (\text{RENEST} \times \text{CLUTCH}_2 \times \text{NEST}_2)] \times (0.5 \times 0.93 \times \text{CHICK})$$

where subscript, i , denotes the age-class, and the subscripts 1 and 2 indicate parameter estimates associated with first nesting and renesting attempts, respectively. Two adjustment factors were used to account for the assumed 1:1 sex ratio at hatch (0.5) and egg hatchability (i.e., 1-[the proportion of infertile and unhatched embryos / total clutch size]) which was fairly constant at 0.93 (SE = 0.01). Total reproductive output for a given age-class (F_1 , F_2) was combined with survival rates of juveniles (P_0) (Fig. 1).

The arithmetic rate of population change (λ), stable age (w), reproductive value (v), and sensitivity analyses were derived using algorithms (Caswell 2001) in MATLAB® 6.5 software (Mathworks Inc.). Confidence limits (95%) around the observed λ , were calculated using the parametric bootstrap method (Manly 1997, Ebert 1999, Fieberg and Ellner 2001). Bootstrapped λ values were calculated as follows: 1) resample lower-level vital rate from a probability distribution (i.e., beta-distribution for

probabilities, and normal distribution for continuous variables), 2) parameterize the projection matrix of resampled rates, 3) calculate λ from the re-parameterized matrix, and 4) repeat 1,000 times. If $\lambda = 1$ in the upper or lower 2.5% then the null hypothesis of population stability was not rejected.

Retrospective analysis

A life table response experiment (LTRE) was used to quantify the contribution of actual variation of these rates on the variability in λ between the two populations (Caswell 1996). I use superscript ‘I’ and ‘II’ to indicate matrices or parameter estimates from Areas I and II, respectively. In a fixed effect, single class design the mean matrix, $\mathbf{A}^{(.)}$, can be parameterized from two populations [$\mathbf{A}^{(.)} = (\mathbf{A}^{(I)} + \mathbf{A}^{(II)}) / 2$] and one can evaluate the partial derivatives of the mean matrix. In order to quantify the lower-level contributions of two matrices this ‘effect’ of treatment II on λ can be decomposed by,

$$\lambda^{II} - \lambda^I \approx \sum_i (x_i^{II} - x_i^I) \frac{\partial \lambda}{\partial x_i}.$$

This type of LTRE assumes that \mathbf{A} may be reparameterized in terms of the lower-level rates (x_i) (Caswell 1996). In practice the difference in an elasticity value of a given rate (a_{ij}) is multiplied by the sensitivity (s_{ij}) value of the mean matrix. This results in elasticity values (e_{ij}) that describe the contribution of or variation explained by a lower-level vital rate to the observed rate of population change.

Prospective analyses

Prescriptions for targeting management actions were ranked using sensitivity and elasticity analyses. Elasticity values were derived analytically to compare the proportional effect of infinitesimal changes in a vital rate to λ . Elasticities (e_{ij}) of the

matrix elements are scaled (log) sensitivity values (s_{ij}) so that they sum to 1 (Caswell 2001),

$$e_{ij} = \frac{\partial(\log \lambda)}{\partial(\log a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}.$$

However, matrix elements, F_1 and F_2 , were comprised of several lower-level rates (x_i). The contribution of these rates to λ were evaluated by taking the partial derivatives of the matrix (Caswell 2001),

$$\frac{x}{\lambda} \frac{\partial \lambda}{\partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}.$$

This gives the proportional change in λ from a proportional change in a lower-level rate (x). I also used variance scaled sensitivities (VSS) as a measure of vital rate elasticity, because scaling (i.e., arcsin-square root transform in this study) associated with VSS allows for an evaluation of a given change in a vital independent of the actual parameter value (Link and Doherty 2002). Link and Doherty (2002) define prospective analyses as the functional dependence of λ on x_i , and the mean/variance relation for any random variable distributed on the unit interval suggests that VSSs based on the arcsine square root transform are more appropriate for demographic probabilities (θ) where,

$$\text{VSS} = \frac{\partial \log \lambda}{\partial [2 \sin^{-1}(\sqrt{\theta})]} = \left(\frac{\sqrt{\theta(1-\theta)}}{\lambda} \right) \frac{\partial \lambda}{\partial \theta}.$$

I report both standard elasticities and VSSs for comparative rankings to other studies.

Perturbation analysis

As a compliment to the elasticity matrix and lower-level contributions, perturbation analyses were used to identify future management alternatives (i.e., prescriptions) that would have the greatest impact on the populations (Mills et al.1999).

The four most important vital rates, as determined from a ranking of the VSSs were selected for the perturbation analyses. I took two slightly different approaches to evaluate conservation alternatives. First, I used a life stage simulation analysis (LSA) (Mills et al. 1999) approach where the mean of a vital rate was increased by 10, 20, and 30% and its variance reduced by 10%. This method assumes that current estimates of vital rates are unbiased. Second, I set a specific management target for each vital rate, and examined what effect that rate had on λ . This modified LSA requires that the mean of a rate of interest increase by a fixed amount and simultaneously reduce variability in the rate (~10% in this study). Simulations for both perturbations were conducted similar to the parametric bootstrap for confidence limits, except that the vital rate under assessment was drawn from a uniform distribution with its respective mean and range (Wisdom et al. 2000), and all other rates were drawn from the appropriate probability distribution. Under the management target simulations both NEST and CHICK were set to have a probability of 0.3, and 0.4; and PBS and HEN were set to have a mean of 0.5, and 0.6 and a range of ± 0.1 . I constrained perturbations to the stated probabilities as these rates are similar to those reported for the species and its congeners (Schroeder and Robb 1993, Giesen 1998). The effectiveness of a proposed management action was assessed by the proportion of bootstrap replicates in a simulation where $\lambda \geq 1$. It was assumed that most management of lesser prairie-chicken populations would not be age-specific, and would affect all age-classes in a similar manner. Thus, in these simulations for NEST and HEN both yearling and adult females were drawn from the same probability distribution.

RESULTS

Vital Rates

Clutch sizes were markedly different between first (12.1 eggs) and renests (7.7 eggs) and a similar pattern was observed at both areas (Table 3). Nest success varied between areas (Table 3) but most of the variability was accounted for by the greater probability of first nests (14–41%) being successful than renests (12–14%). The probability of renesting after nest loss was not equal between areas (Table 3). Daily survival rates of 34-day old chicks was similar between the areas (Table 3), although samples sizes were small. Known-fate survival of females varied by area and age-class with the yearling to two-year old transition having 13-15% higher survival than older birds (Table 3).

Projection Matrices

The parameterized matrices reflected the age-structure and differences in rates between the two areas,

$$A^{(I)} = \begin{vmatrix} 0.289 & 0.144 \\ 0.429 & 0.302 \end{vmatrix}$$

$$A^{(II)} = \begin{vmatrix} 0.224 & 0.284 \\ 0.588 & 0.438 \end{vmatrix}.$$

The arithmetic rate of population change was markedly different between the two populations $\lambda^{(I)} = 0.544$ (95% CL = 0.28, 0.85) and $\lambda^{(II)} = 0.754$ (95% CL = 0.47, 1.00).

The confidence limits indicated that Area I was declining and Area II was not significantly different from $\lambda = 1.0$. The dominant left and right eigenvectors of the matrix determined the reproductive value (\mathbf{v}) and stable-age distribution (\mathbf{w}) of the population, respectively. Adults comprised the majority of the stable-age distribution

vector (\mathbf{w}) on Area I (0.66) and Area II (0.65). Adults on the Area II had a higher reproductive value ($\nu = 0.90$) than Area I ($\nu = 0.59$).

Retrospective analysis

Using Area I as the reference population, the effect of area on λ was $\lambda^{(II)} - \lambda^{(I)} = 0.21$. There were positive contributions from advantages in $HEN_{y,a}$ on Area II, especially for the 2+ age-class (Fig. 2). There was also a positive contribution from the advantage of $NEST_{1a}$ on Area II, and it was the largest contribution overall. There was a negative contribution from an advantage for CHICK on Area I (-0.09) and was the 2nd largest overall contribution. Thus, most of the variability in $\lambda^{(II)} - \lambda^{(I)}$ can be explained by higher nest success on Areas II, higher chick survival on Area I, and to a lesser extent higher $HEN_{y,a}$ on Area II.

Prospective analyses

Elasticity values of the projection matrices (upper-level elasticities),

$$E^{(I)} = \begin{vmatrix} 0.259 & 0.228 \\ 0.228 & 0.285 \end{vmatrix}$$

and

$$E^{(II)} = \begin{vmatrix} 0.111 & 0.263 \\ 0.263 & 0.364 \end{vmatrix},$$

indicated that future changes in HEN_a would have the largest effect on λ . Apparently, the overall future reproductive contribution of F_I on Area II was relatively small. Analytic elasticity values for the lower-level rates suggested that λ was most sensitive to future changes in the rates PBS, CHICK (both ranked first), and HEN_a (ranked second) in these populations (Table 4). Ranked as third largest effect on rates of population change were

$HEN_y (\lambda^{(II)})$ and $NEST_{1y} (\lambda^{(I)})$. Renesting contributed little to future changes in λ . The top four ranks for VSSs were consistent with analytic elasticities except for Area II. However, on Area I, $NEST_{1y}$ and HEN_y were not ranked in the top 4, but $NEST_{1a}$ was included. Variance scaled sensitivities reprioritized the importance of $e(PBS) = e(CHICK)$ and each having the largest effect on λ , to CHICK having the single largest contribution to changes in λ . Interestingly, VSS ranking reduced PBS to a rank of third for both populations, and $NEST_{1a}$ ranking increased to second for Areas I. Conversely, the ranking of HEN_a and $NEST_{1a}$ dropped to fourth for Area I and II, respectively.

Perturbation analysis

The perturbation analysis simulated management practices that would presumably yield large changes in λ with respect to the targeted vital rate (Mills et al. 1999). The lower-level VSSs indicated $NEST_1$, CHICK, PBS, and HEN were the most important rates with respect to changes in λ , and were used in the perturbation analyses. Hypothetical management scenarios for $NEST_1$ and CHICK were assumed to respond the greatest from habitat management. Practically, variables such as residual cover (Buhnerkempe et al. 1984) and forb abundance are important to probability of success of these two life stages (Riley and Davis 1993). Manipulations to PBS and HEN were surrogates for limiting (+10%) or eliminating (+20 and 30%) the hunting season as this is typical management for increasing annual survival rates of exploited populations (although its effectiveness is largely untested). Alternatively, stochastic events and landscape factors that affect natal dispersal could also impact PBS.

Absolute increases in vital rates had little impact on λ (Table 5). Neither population had large increases in λ for changes in single rates, and < 19% of any

simulation had $\lambda \geq 1$. Suggesting that relatively large changes in vital rates are required to have any measurable effect on λ . Increases in PBS and NEST₁ + CHICK had the largest impact on both populations but neither treatment at + 30% was large enough to maintain population stability more than 18% of the time. Future increases in PBS had the greatest effect on $\lambda^{(I)}$ as was predicted by the elasticity values. Interestingly, the vital rates CHICK and HEN, which had the highest rank in the VSS analysis with respect to their effects on $\lambda^{(II)}$, responded poorly to reductions in harvest or other management practices that might increase these survival rates. Management that simultaneously manipulated both NEST₁ + CHICK rates had far more effect on λ than did changes in HEN.

The results of the simulated management scenarios (Table 6) complemented the LTRE and to a lesser extent the lower-level elasticity analysis. The perturbations indicated that $\lambda^{(I)}$ responded most to habitat management that increased NEST₁ + CHICK to 40% and relatively less to increases in PBS and HEN. However, if targeting a single vital rate, HEN had the largest impact on $\lambda^{(I)}$. Management that simultaneously targeted both NEST₁ + CHICK rates at 40% had nearly twice effect on $\lambda^{(I)}$ (Table 6) than did managing for HEN of 60% (66 and 100% increase of the current rates). Management scenarios with respect to $\lambda^{(II)}$ indicated that CHICK = 40% had the largest single impact on $\lambda^{(II)}$. HEN and PBS had a greater effect on $\lambda^{(II)}$ than did NEST₁. It is not surprising then that NEST₁ + CHICK had the largest effect on $\lambda^{(II)}$.

DISCUSSION

Parameter estimates

This study yielded several important results about the demography of lesser prairie-chickens and illustrated some of the more complementary sensitivity analyses (Mills et al. 1999, Wisdom et al. 2000). I am confident of the estimates of female survival, post-brood survival and nest success in this study, because radiomarking does not appear to affect survival negatively (Chapter 2). High rates of censoring ($> 20\%$) can positively bias known-fate survival estimates when sample sizes are small (< 50 animals) (Tsai et al. 1999). Right-censoring of adults and yearlings in this study was $\sim 30\%$, and may have biased my estimates. Alternatively, right-censoring of juvenile birds during post-brood survival was low (6.3%) and those estimates are likely accurate, albeit from 32 birds over 3 years. Nest success in this study was similar to estimates in the literature (Giesen 1998). Females were flushed only once during incubation to determine clutch size. Westemeier et al. (1998) reported that flushing greater prairie chicken females from nests resulted in 95% of those females returning to nests, and nest success was not negatively impacted. It is possible that estimates of CHICK were biased low due to systematic flushing; however, $> 33\%$ of all broods in this study suffered complete brood loss prior to the first flush at 14-days post-hatch. Most flush-counts were conducted in the morning while chicks were being “brooded” by the female, thus detection probability was likely high. As chicks reached 34 days of age, their mobility and independence was such that they could mix readily with other broods and it is possible that estimates of CHICK were biased low later in the sampling period. Small sample sizes were the greatest limitation in estimating this rate.

Age-structure was most prominent in survival rates when compared to the other rates in the populations, as the transition from yearling to adult age-class was the highest rate on both areas. This pattern of high yearling survival also occurred in banded males during this study (Chapter 1), and reflected a life-history strategy of a “short-lived large clutch size species” (Saether and Bakke 2000). Yearling males exhibited different breeding behaviors in terms of site fidelity, which may have increased survival to a second year. Similarly, yearling females may not be as tenacious in nest-defense leading to less mortality during incubation (Chapter 3).

Projection matrix

Population assessment.—The stable age distribution (w) projected by the matrix was similar to the actual age-structure of the radiomarked sample for both areas (yearling = 0.38, adult = 0.62). Meeting the assumption of w in the model is important especially when reproductive values (v) are unequal in the population (Hoekman et al. 2002), as was the case in both of my populations. The λ 's projected 25-46% declines, but only Area I was significantly different from $\lambda = 1$. Age-ratios (0.27-0.786 yearling/adult) during spring trapping suggests either recruitment from outside the study area or negative bias in estimated rates of reproduction. The confidence limits around λ in both populations suggested that in fact this rate was similar between areas. The large range of confidence limits resulted because my parameter estimates also included sampling variance. Longer-term studies can separate process and sampling variance and yield estimates that are more precise. Although, the confidence bands around λ suggested no differences in these populations, vital rates contributing to these observed values were quite different.

Past variability and LTRE

Population diagnosis.— LTRE has not been used previously in demographic studies of grouse or in other conservation literature (Caswell 2001); thus comparisons within or outside this taxon is not possible. Although a powerful tool, I was limited in my analysis by having only 2 sites for comparisons. A larger number of study areas or an experimental design in which one or both areas were manipulated (and pre- post-treatment matrices were parameterized and compared) would have provided greater resolution in the analysis.

The LTRE analysis has two important points. First, the area effect on λ was relatively large (0.21) because fragmentation and habitat loss may have had an effect on vital rates. These contributions were several orders of magnitude larger in the case of NEST₁ but less so for CHICK with respect to the area effect. Thus, statistically insignificant differences in λ do not necessarily equate to equal dynamics within populations (Caswell 1996, Johnson and Braun 1999). Second, decomposition of the contributions to λ with respect to the lower-level rates specified the aspects of F_i that were important to each population, CHICK, PBS, and NEST₁. This provided some insight as to why λ may not have been equal between populations. The habitat and landscape features differed between these areas. Vegetation only differed slightly in terms of overall sagebrush density; however Area II had 2 pastures with the highest densities ($>9,000$ plants ha^{-1}) and highest probability of nest success. Modeling of chick survival indicated that moderate stands of sagebrush ($4,000 - 6,000$ plants ha^{-1}) yielded the highest daily survival rate (DSR) of chicks through 14-d post-hatch (Pitman 2003). Forty percent and 10% of the pastures on Area I and II, respectively, had density

estimates within this range, suggesting that the elevated chick survival on Area I may have been explained in part by the prevalence of optimal sagebrush density.

There was substantially more human disturbance (i.e., within patch fragmentation) on Area I and may have resulted in reduced fecundity and survival compared to Area II. Habitat fragmentation has an array of detrimental demographic effects (Knick and Rotenberry 1995), some of which were potentially borne out in this study. However, without the appropriate replicates, I can only discuss the implications for these two sites. The higher density of pump-jacks, buildings, and length of road on Area I yielded a more highly fragmented habitat (Table 1) that could have had negative impacts on survival or reproductive output. The confounding factors of habitat structure and landscape features will require future work to differentiate any causal relationships.

Past variation in vital rates may be important to understanding future changes to the matrix (Wisdom et al. 1999). The LTRE in this study elucidated the vital rates in each population that were contributing to the observed differences in λ . This suggests that past differences in habitat or landscape may have contributed to these differences in nest success and chick survival.

Prospective analyses (prescriptions)

Analytic perturbations.—Variance scaled sensitivities indicated that the functional relationship of λ on CHICK was ≥ 2.1 times larger than any other rates for Area II and nearly so (≥ 1.7) for Area I. I concur with the assertion of Peterson et al. (1998) that the sensitivity to CHICK should have a greater population-level impact because total brood loss for a female results in no contribution of young that year. Total clutch loss of first nests may have a similar effect, but there is a probability of renesting.

The VSS of HEN_a and $NEST_{1a}$ indicated that future changes in these rates had the second largest impact on $\lambda^{(II)}$ and $\lambda^{(I)}$, respectively. This may result in part from a higher sensitivity of λ to changes in nest success of older birds, because >30% of all female mortality occurs during the nesting season (Chapter 3). Thus, steps taken to ensure increases in nest success will likely also increase female survival. Additionally, yearlings have the highest survival rates going into the second breeding season where nest success was highest, thus yielding a relatively high reproductive value ($v^{II} = 0.9$) and sensitivity. PBS was valued similarly in both populations having the third largest effect on λ . The importance of PBS to these populations may be two-fold: 1) it is an index to the limitations of the actual recruitment rate, and 2) if the observed λ 's do indicate declining populations, then PBS may also reflect the sensitivity of λ to immigration from other habitat patches. First, Peterson and Silvy (1994) found that reproductive success could predict the numbers of prairie chickens on leks the following spring, and Wisdom and Mills (1997) found the survival of the first age-class was most important to simulated population trends. My findings support these suggestions and perhaps provide a generalized life-history strategy for prairie chickens, a life-history strategy of “boom or bust” fecundity. Such a strategy may drive short-term dynamics in a short-lived large clutch size organism. Second, PBS of radiomarked juveniles in my study is merely a survival rate (S). However, at the population level PBS is comprised of two rates, S and immigration or dispersal from other habitat patches. Because natal dispersal lesser prairie-chicken often occurs just prior to the breeding season (Pitman 2003), new individuals could be added to the population without experiencing the extrinsic factors of either of my study areas. Given the declining λ 's of these populations, it is not surprising

that the vital rate that has a component somewhat independent of local constraints (and directly adding to the population size) would be projected to have a relatively large impact on population stability.

Comparisons to other grouse species.—Previous sensitivity analyses on 6 grouse species have yielded mixed results (Table 7 and 8). Upper-level elasticity analyses tended to rank survivorship of older birds higher than fecundity values (Table 7). This was surprising for Attwater's and greater prairie-chickens as their clutch size is markedly larger (13 vs. 8 eggs) than that of the longer-lived greater sage-grouse and black grouse. However, survival of juveniles to the first breeding (PBS in this study) was consistently ranked highly among upper-level elasticities. This reiterates the importance of recruitment both in terms of local survival and probability of immigration of the juvenile age-class. I examined and ranked 4 lower-level elasticities that were comparable (e.g., nest success, chick survival, post-brood survival, and adult survival) across 4 studies including my own (Table 8). This summary revealed that chick and PBS were generally the first and second most important rates contributing to λ , respectively. This was surprising given that capercaillie and willow ptarmigan have relatively small clutch sizes compared to prairie grouse, because one would predict that λ would be most sensitive to changes in adult survivorship in these longer-lived species.

Simulated perturbations.—Discrepancies between elasticity and perturbation analyses was expected to some degree based on an intensive simulation study (Mills et al. 1999). Mills et al. (1999) provided evidence that infinitesimal and proportional changes in a matrix do not reflect real changes in the environment of a species. They argue that environmental stochasticity or management plans can potentially generate disproportional

and large changes in several rates simultaneously, yielding different inference about vital rates of a population than elasticity analysis. Several studies (Mills et al. 1999, Heppell et al. 2000, Link and Doherty 2002, Nichols and Hines 2002) have concluded that elasticity analysis was inadequate as a stand-alone result and incorporating other sensitivity indices may yield a more complete understanding of the system. The lower-level elasticities were weighted heavily towards adult survival and post-brood survival in this study. This may have been due in part that the observed λ was <1 and declining populations tend be more sensitive to adult survivorship. The perturbation analysis provided evidence in the opposite direction indicating that nesting and brood rearing aspects of the life history were critical to maintaining population stability for lesser prairie-chickens in southwest Kansas. The importance of these early life stages was echoed in the LTRE as mentioned above. Thus, increases in adult survivorship or post-brood survival by eliminating hunting ($<5\%$ of all current mortality) would do little to stabilize these populations. However, hunting of a declining population can only be justified if it is compensatory to annual survival. This was contrary to the findings of Steen and Erikstad (1996) and Johnson and Braun (1999); both studies found that decreases in adult survivorship from hunting negatively affected population growth, especially in years with poor recruitment. However, the markedly higher harvest rates in those studies likely had a larger effect on survival than that observed in my study.

Conclusions

Population prognosis.— Ascertaining the status of these populations was difficult given that both sampling and process variance were included in the parameter estimates. However, efforts to increase nesting success and chick survival are paramount, and the

former likely will increase female survival. The tenuous stability of λ in these two populations suggests that these fragmented populations are maintained in part by immigration. Lek survey routes through this region have not detected the declines reported here (KDWP unpublished data), and age-ratio data collected during this study support the idea that immigration is a potential mechanism for population stability. It is noteworthy that the results of this comprehensive field study reflected the conclusions of other workers on prairie grouse (Peterson and Silvy 1994, Wisdom and Mills 1997, Peterson et al. 1998) that extracted rates from the literature and across large geographical regions. It is clear from this study and other modeling exercises (Wisdom and Mills 1997, Peterson et al. 1998) on prairie grouse that nesting and brood rearing are the critical rates to maintaining population stability. This study also indicated the importance of immigration via post-brood survival from other habitat patches. Management efforts aimed at increasing the quality, and/or quantity of nesting and brood habitat will have the greatest benefits to lesser prairie-chicken populations. Alternatively, this study provided some initial insight as to the impacts of hunting on a declining species, and indicated that eliminating hunting (if additive) would not yield a stable population.

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Table 1. Habitat and landscape features for study areas I and II in southwestern Kansas, 1998-2003. Parameter and standard errors (in parentheses) presented when a variable was not directly measured.

Habitat feature	Area I	Area II
Fragment size (ha)	5,684	5,660
Sagebrush density (ha^{-1})	3,611 (689)	4,206 (697)
Sagebrush height (cm)	57 (5.7)	55 (5.9)
Sagebrush diameter (cm)	76 (9.9)	66 (12.5)
Road (km)	154.7	129.2
Powerline (km)	28.4	30.8
Pump-jack ($\text{ha}^{-1,000}$)	10.6	6.9
Buildings (n)	6	1

Table 2. Parameters for demographic model of female lesser prairie-chickens.

Parameters describe events occurring within each time step (1 Apr in year t to 1 Apr in year $t + 1$).

Parameter	Definition
CLUTCH ₁	Average number of eggs in first nesting attempt.
NEST _{1y}	Probability of a yearling's nest hatching at least one egg.
NEST _{1a}	Probability of an adult's nest hatching at least one egg.
RENEST	Probability that a female will renest in the event the first nest is predated (# of renests / total # of failed nests)
CLUTCH ₂	Average number of eggs in second nesting attempt, if first nest fails.
NEST ₂	Probability of a renest hatching at least one egg.
CHICK	Probability that a chick will survive from hatch to 34-d post-hatch.
PBS	Post brood survival (PBS) probability a chick survives from 34-d post-hatch to first spring.
HEN _y	Probability a yearling female will survive from t to $t + 1$.
HEN _a	Probability an adult female will survive from t to $t + 1$.

Table 3. Parameter estimates (θ) of vital rates of yearling (Y) and adult (A) lesser prairie-chickens radio-marked in Finney County, Kansas 1998-2002. Vital rates are defined in Table 2.

Vital rate	Area I		Area II		
	Y $\theta \pm \text{SE}^a$	A $\theta \pm \text{SE}$	Y $\theta \pm \text{SE}$	A $\theta \pm \text{SE}$	Pooled $\theta \pm \text{SE}$
NEST ₁ ^b	0.303 \pm 0.080 (33) ^c	0.140 \pm 0.053 (43)	0.320 \pm 0.093 (25)	0.415 \pm 0.077 (41)	--
NEST ₂	0.143 \pm 0.163 (14)		0.125 \pm 0.080 (16)		--
RENEST	0.223 \pm 0.055 (60)		0.410 \pm 0.079 (39)		--
CLUTCH ₁	--	--	--	--	12.1 \pm 1.6 (151)
CLUTCH ₂	--	--	--	--	7.7 \pm 3.0 (29)
CHICK	0.293 \pm 0.131 (12)		0.209 \pm 0.080 (26)		--
PBS ^c	--	--	--	--	0.539 \pm 0.089 (32)
HEN	0.429 \pm 0.117 (24)	0.302 \pm 0.080 (50)	0.588 \pm 0.100 (33)	0.438 \pm 0.083 (48)	--

^a Clutch sizes were reported with ± 1 standard deviation, all probabilities with ± 1 standard error, and sample sizes are in parentheses.

^b All parameter estimates except for hen survival were calculated from field data gathered between 1998 and 2002. Annual hen survival was only estimated from 2000 to 2003.

^cThe estimates of clutch sizes (CLUTCH_{1,2}) and post-brood survival (PBS) were pooled across areas and age-classes due to constancy of rates, and sample sizes, respectively.

Table 4. Analytic elasticities and variance scaled (arc-sin) sensitivities (VSS) for lower-level vital rates of matrix.

Vital rate ^a	Area I		Area II	
	Elasticity	VSS	Elasticity	VSS
NEST _{ly}	0.24	0.37	0.10	0.15
NEST _{la}	0.20	0.49	0.24	0.29
RENEST	0.05	0.11	0.03	0.08
NEST ₂	0.05	0.09	0.03	0.04
CHICK	0.49	0.76	0.37	0.73
PBS	0.49	0.45	0.37	0.35
HENy	0.23	0.26	0.26	0.22
HENa	0.29	0.43	0.36	0.41

^a Vital rates defined in Table 2.

Table 5. Results of a life stage simulation analysis (LSA) in which each vital rate was increased by 10, 20, and 30 % (of its current estimate) and its variability decreased by 10%. The proportion of simulated matrices ($n = 1,000$) for each vital rate and percent increase that resulted in $\lambda \geq 1$, is a measure of management effectiveness.

Area / rate increase	Vital rates (Proportion of 1,000 simulations where $\lambda \geq 1$)				
	NEST	CHICK	NEST + CHICK	PBS	HEN
Area I					
10%	0.009	0.007	0.014	0.082	0.010
20%	0.018	0.010	0.032	0.127	0.005
30%	0.027	0.015	0.059	0.180	0.007
Area II					
10%	0.026	0.037	0.048	0.062	0.029
20%	0.037	0.066	0.072	0.116	0.057
30%	0.059	0.079	0.133	0.174	0.082

Table 6. Results of a modified LSA in which each vital rate was targeted for a set rate of 30 and 40% for nesting and chick survival, and 50 and 60% for post-brood survival and female survival. Variability was simultaneously decreased by ~20% for each rate. The proportion of simulated matrices ($n = 1,000$) for each vital rate and its management goal that resulted in $\lambda \geq 1$, is a measure of management effectiveness.

Area / targeted rate	Vital rates (Proportion of 1,000 simulations where $\lambda \geq 1$)				
	NEST	CHICK	NEST + CHICK	PBS	HEN
Area I					
30 (20-40)%	0.009	0.000	0.001	ND ^a	ND
40 (30-50)%	0.059	0.005	0.140	ND	ND
50 (40-50)%	ND	ND	ND	0.015	0.035
60 (50-70)%	ND	ND	ND	0.036	0.089
Area II					
30 (20-40)%	0.004	0.098	0.029	ND	ND
40 (30-50)%	0.032	0.286	0.365	ND	ND
50 (40-50)%	ND	ND	ND	0.015	0.041
60 (50-70)%	ND	ND	ND	0.077	0.081

^a ND = no data recorded for these simulations.

Table 7. Ranks of upper-level elasticities from matrix elements for 4 grouse species. A rank of 1 indicates the most important matrix element.

Species	Ranks of upper-level elasticity ^{a,b}						Reference
	F ₁	F ₂	F ₃	P ₀	P ₁	P ₂	
Black grouse	4	3	ND ^c	2	1	ND	Caizergues and Ellison 1997
Greater sage-grouse	6	5	3.5	2	3.5	1	Johnson and Braun 1999
Greater prairie-chicken	3	4	6	1	2	5	Wisdom and Mills 1997
Lesser prairie-chicken ^d	4	2.5	ND	ND	2.5	1	This Study
Lesser prairie-chicken ^e	4	2.5	ND	ND	2.5	1	This Study
Average ranks ^f	4.2	3.4	4.8	1.7	2.3	2.0	--

^a Ranks of one-half (0.5) indicate a tie in elasticity values, and each was given 0.5 and the next rank was not used (e.g., a tie of 3 = 3.5, 3.5, 5, 6).

^b Matrix elements are as follows F₁- F₃ = fecundity arcs for yearling to 3yr old females, and P₀- P₂ = survival (transition) probabilities of juvenile to yearling (P₀) through 2 year old to 3 year olds (P₂).

^c ND = no data available.

^d Area I in this study.

^e Area II in this study.

^f Ranks were averaged to summarize the importance of each rate across species.

Table 8. Ranks of lower-level elasticities from matrix elements for 4 grouse species. A rank of 1 indicates the most important vital rate.

	Lower-level elasticity ranks ^a				Reference
	Nest success	Chick	PBS	Adult	
Willow ptarmigan	5	4	1	2.5	Steen and Erikstad 1996
Attwaters prairie-chicken	3	1	4	2	Peterson et al. 1998
Capercaillie	3	1	ND ^e	2	Grimm and Storch (2000)
Lesser prairie-chicken ^b	3.5	1	3	5	This Study
Lesser prairie-chicken ^c	5	1	3	3.5	This Study
Average ranks ^d	3.9	1.6	2.8	3	--

^a Ranks of one-half (0.5) indicate a tie in elasticity values, and each was given 0.5 and the next rank was not used (e.g., a tie of 3 = 3.5, 3.5, 5, 6).

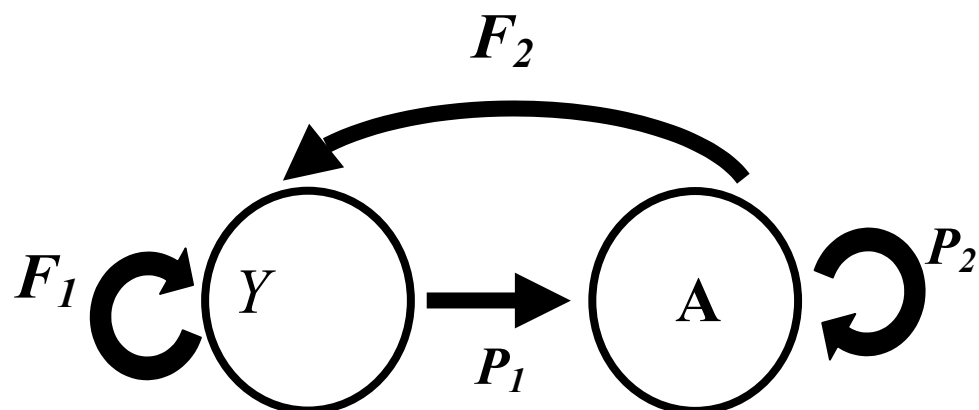
^b Area I in this study.

^c Area II in this study.

^d Ranks were averaged to summarize the importance of each rate across species.

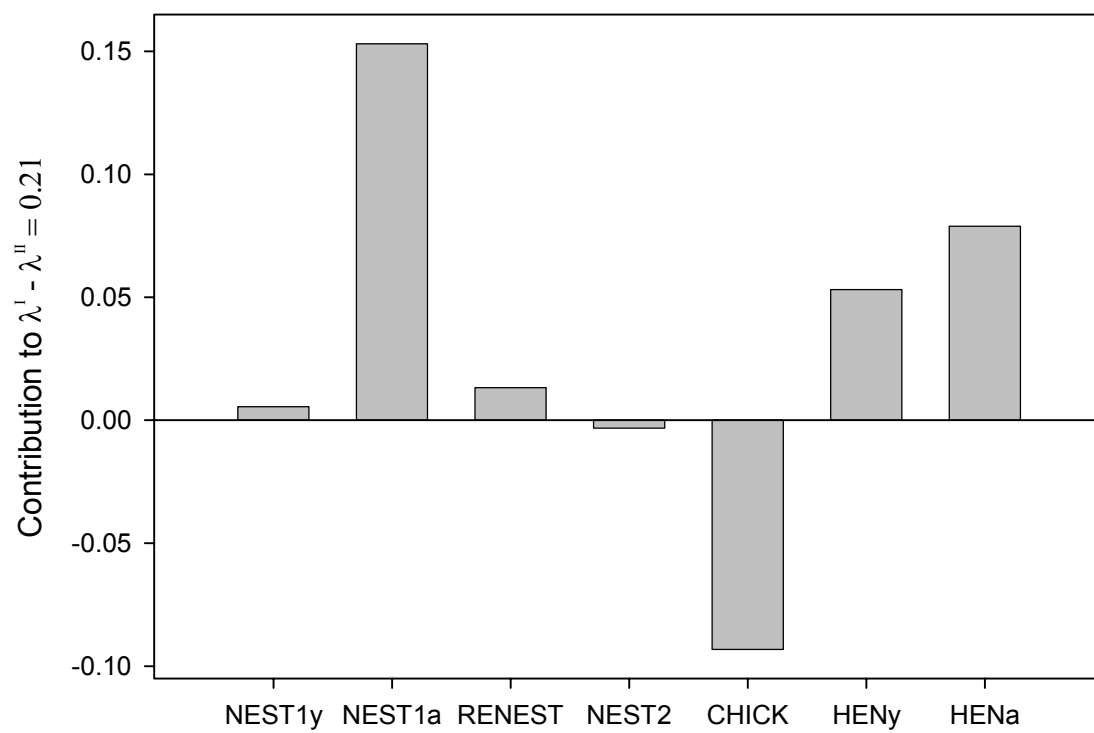
^e ND = no data available.

Fig. 1. Life-cycle diagram and matrix for a 2 age-class pre-breeding model of female lesser prairie-chickens. Notations for vital rates are defined in the text.



$$A = \begin{bmatrix} F_1 P_0 & F_2 P_0 \\ P_1 & P_2 \end{bmatrix}$$

Fig. 2. Results of the life-table response experiment (LTRE) show the contribution of each vital rate to the difference in λ between Area I (lower half of panel) and Area II (upper half of panel). This retrospective analysis determined that advantages of NEST_{1a} and CHICK on Area II and I, respectively, had the largest contribution to population growth. Notations for vital rates are defined in the text.



CHAPTER 5

THE EFFECTS OF LANDSCAPE FEATURES ON LESSER PRAIRIE-CHICKEN HABITAT USE

Abstract: Suitable habitat for the lesser prairie-chicken (*Tympanuchus pallidicinctus*) has been reduced markedly over the past 100 years. The remaining habitat is widely used for petroleum exploration and extraction, cattle grazing, powerline easements, and the generation of electricity. Given the tenuous status of the species and the demands on land use for its remaining habitat, it is imperative that suitable habitat be quantified for impact assessment and conservation planning. I examined the relationship of several habitat characteristics and landscape features as they pertained to habitat suitability in southwestern Kansas. I quantified these characteristics in use and non-use areas as determined from the presence or absence of prairie chicken locations determined by radiotelemetry data from 1997 to 1999. I extended the analysis and quantified the proportion of landscape features and sagebrush density in monthly-ranges of radiomarked birds 2000 to 2002. The MANOVA results indicated habitat selection by prairie chickens. Canonical variates analysis resulted in 87 and 13% of the data explained by canonical variates-1 and -2, respectively. Canonical variate-1 was positively correlated with sagebrush density, cover, and diameter, but negatively correlated with distance to wells and structures. This linear combination best described absent-sites. Canonical variate-2 had the strongest positive correlation with distance to powerline, and best described use-sites. The average odds of a powerline occurring in a non-range were 3.22 times more likely than in a monthly-range. Monte Carlo simulations of distances to

structures indicated that the nearest 40% of lesser prairie-chicken centers of use were farther from anthropogenic features than would be expected at random.

INTRODUCTION

Suitable habitat for the lesser prairie-chicken (*Tympanuchus pallidicinctus*) has been markedly reduced over the past 100 years. What remains is highly fragmented throughout the species' range (Giesen 1998). The remaining habitat is widely used for petroleum exploration and extraction, cattle grazing, powerline easements, and the generation of electricity (Jamison et al. 2001a). The cumulative loss of habitat and declining population trends led to the "warranted but precluded" threatened listing under the Endangered Species Act (USFWS 2002). The lesser prairie-chicken's dependency on native rangeland has been well studied, at the microscale (Jones 1963, Crawford and Bolen 1974, Riley et al. 1992, Jamison et al. 2001b), and the macroscale (Jamison 2000, Woodward et al. 2001, Fuhlendorf et al. 2002). Despite these large-scale contractions of habitat and thorough examination of microhabitat variables, little is known about the specific parameters of a suitable habitat patch. Given the tenuous status of the species and the demands on land use for its remaining habitat, it is imperative that suitable habitat be quantified for conservation assessment and planning.

Jamison (2000) examined habitat use of male lesser prairie-chickens as it pertained to selection ratios of sand sagebrush (*Artemisia filifolia*), cropland, and miscellaneous grasslands in southwestern Kansas. Generally, lesser prairie-chickens were tied to sagebrush throughout the year, but exhibited higher selection ratios for this cover-type during the summer months (Jamison 2000). Despite the apparent importance of sagebrush, there were several areas within the prairie fragment (~5,000 ha) in which

radiomarked birds were not located, and unmarked individuals were not flushed or observed in these areas (B. E. Jamison, unpublished data). This lack of habitat use provided an opportunity to quantify both habitat variables and landscape features as they pertain to suitability of lesser prairie-chicken habitat.

The objective of this paper is to examine what suite of habitat characteristics and landscape features determines habitat suitability in southwestern Kansas. I used Jamison's (2000) radiotelemetry location data of male and female lesser prairie-chickens to quantify these characteristics in use and non-use sites as determined from the presence or absence of prairie chicken locations. I extended the analysis in 2000-2002 and quantified the proportion of landscape features and sagebrush density in monthly-ranges of radiomarked females.

METHODS

Study area

The study region was comprised of 2 fragments (~5000 ha each) of native sandsage prairie near Garden City, Finney County, Kansas (37° 52' N, 100° 59' W). Work began on Area I (southwest of Garden City) in 1997. In 2000, trapping and monitoring efforts were expanded to include Area II (southeast of Garden City). Prior to 1970, these 2 areas were part of a contiguous tract of native sandsage prairie. The development of center pivot irrigation left these areas as two fragments with about 19 km of non-habitat between patch centroids (Waddell and Hanzlick 1978). Shrub and grass vegetation in the prairie fragments was comprised of sandsage, yucca (*Yucca* spp.), sandreed grasses (*Calamovilfa* spp.), bluestem grasses, sand dropseed (*Sporobolus cryptandrus*), and sand lovegrass (*Eragrostis trichodes*). Primary forb species in the

region included ragweed (*Ambrosia* spp.), sunflower (*Helianthus* spp.), and Russian thistle (*Salsola iberica*) (Hullett et al. 1988, Jamison 2000).

Field methods

Lesser prairie-chickens were captured on leks using walk-in funnel traps during March and April 1997-2002 (Haukos et al. 1991). Each captured bird was fitted with a lithium battery powered transmitter with a mass < 12-g. During Phase I (1997–1999) males and females were tracked daily from April to September 1997, and April to April 1998–2000. Females were tracked daily from April to April during Phase II (2000–2003). A truck-mounted null-peak twin-Yagi telemetry system was used to triangulate individuals remotely.

Retrospective analysis (Phase I)

Defining use.—I quantified both micro- and macrohabitat variables that occurred in use and non-use areas as determined from Jamison’s (2000) study from 1997 to 1999. Thus, I sampled vegetation in the areas defined below in 2000 and 2001. Use areas were defined from a 95% fixed kernel home range (Worton 1989) of all lesser prairie-chicken locations ($n = 21,363$) that intersected the study area (Jamison 2000). Areas not intersected by this polygon were defined as non-use areas. I defined 2 types of non-use sites: 1) areas adjacent to use sites but where radiomarked birds were never located (hereafter non-use sites), and 2) an area north of the Sunflower Electric Power plant (Area I southwest of Garden City, KS) which was not known to have breeding populations of prairie chickens, and where radiomarked birds were never located (hereafter absent sites). Although I cannot make absolute statements regarding the

avoidance of these areas by lesser prairie-chickens, the data recorded over 6 years never documented radiomarked or unmarked birds in absent and non-use areas.

Sampling.—I generated random points (UTM coordinates) within use-, non-use, and absent areas in ARCVIEW 3.1 (ESRI 1998). Random points were located in the field using a handheld global positioning system (GPS) unit. At each random point, I placed a 1.5×0.5 m quadrat and estimated the percent cover of shrub, grass, forb, and litter. Shrub density ha^{-1} was estimated using a modification of the point center quarter method (Cottam and Curtis 1956), where if the nearest shrub was > 15 m from the random point that quadrant was censored, and density was estimated based upon both the number of distances measured and the number censored (T. Loughin, Kansas State University, unpublished data). This modification was necessary to increase the efficiency of data collection in the field. Distances to the nearest road, powerline, natural gas or oil well-head (hereafter wells), and structure (e.g., dwellings, compressor station, ash-pile or powerplant) from each random point were calculated in a geographic information system (GIS).

Home range estimation and GIS (Phase II)

For the location data from 2000 to 2002 the analyses were extended and quantified the proportion of landscape features and sagebrush density in monthly-ranges of radiomarked females. Azimuths from fixed listening stations were entered into Locate II triangulation software (Nams 2002), and locations of prairie chickens were estimated using Lenth maximum likelihood estimators. Location data were imported into a GIS database of the study area and monthly ranges were estimated using a 95% fixed kernel (Worton 1989) in ARCVIEW 3.1. I limited my sample to those birds that had ≥ 20

locations per month. While this reduced the number of observational units, it ensured that observed range sizes were likely representative of the area covered in a month relative to birds with fewer locations. This also limited the season for which such an analysis could be conducted as the season progressed the number of individuals tracked decreased and premature battery failure also contributed to reductions in sample size. Thus, I chose to focus the analysis on times of the year (April to September) when samples were relatively large and coincided with a peak usage of sagebrush habitats (Jamison 2000). All female locations that occurred on nest sites were excluded as the relationship between nesting and these variables has already been examined (Pitman 2003).

Locations of wells, roads, powerlines, and structures were digitized into the GIS. Monthly ranges for each bird were computed separately for year and month (e.g., Apr 2000) to control for yearly and biological variation in monthly habitat use. The ranges for all birds in a given year and month were combined into a single overall “use range” which was overlaid onto the study area. Each year and month layer (hereafter a monthly-range) was used as a sampling frame to calculate the number of wells, roads, powerlines and structures falling within and outside of (hereafter non-ranges) prairie chicken monthly-ranges. Wells could be counted directly, however, roads and powerlines could not. Thus, following the procedure of Marcum and Loftsgaarden (1980) 244,000 random points were generated within each of the study area polygons and the number of points that intersected roads and powerlines in use and non-use areas tabulated. This resulted in count-data that could be input into contingency table or Poisson rate regression analyses.

Analysis

Retrospective analysis of use.—A fixed model MANOVA (PROC GLM: SAS) was used to examine habitat use for a community of variables (Johnson 1998). This model allowed me to compare the effect of habitat characteristics and landscape features on use simultaneously. I used MANOVA as a conservative approach to multiple comparisons, and to examine the dimensionality of the alternative hypothesis using canonical variates analysis (Johnson 1998). Thus, I reported the means and standard errors of habitat and landscape variables, and their resulting *P*-values from multiple comparisons. I examined the possibility of explaining these sites in a reduced parameter space (i.e. the dimensionality of the alternative hypothesis). The dimensionality of $H_0 = 3$, and $H_a < 3$ in this study. If the population means lie in a subspace (data reduction) then linear combinations (canonical variates) can be used to explain the relationship between use, non-use, and absent sites. I tested the differences in mean canonical variates using differences of means and 95% confidence limits around the differences, and the degree of overlap of 95% ellipses in a 2-dimensional space (canonical variate-1 \times canonical variate-2). The approximate 95% ellipses were estimated as

$$\frac{\sqrt{\chi_{\alpha,k}^2}}{n},$$

where χ^2 = chi-square value at $\alpha = 0.05$, k = number of dimensions, n = number of populations, and if $k = 2$ then the ellipses are circles.

Six habitat variables were included in analyzing use, non-use, and absent sites: percent cover estimates for sagebrush, grass, forb, and litter; shrub density, and shrub diameter. Distances from random points (within the areas defined above) to the nearest

structure, well, powerline, and road (included both paved and unimproved trails) were also included in the analysis.

Monthly-ranges and use.—In the following analyses it is important to recognize that monthly usage included repeated measures on individual birds. This limits my inference and may increase my Type I error rate if certain individuals had a propensity to remain farther from these features than the population mean. However, only 60% of the birds had consistent repeated measures through the sampling period, making a repeated measures design impractical. Thus, I treated monthly-range as the observational unit and blocked on month. Because the goal of the analysis is not to differentiate the variation in usage across months but to examine general patterns of use as it pertains to these landscape features, I assessed the effects on use and controlled for the monthly variability by blocking on month.

I used $2 \times 2 \times K$ contingency tables and Poisson rate regression to examine the relationships between monthly-ranges and the proportion of each area occupied by powerlines, roads, and wells controlling for months there were 6 blocks in 2000 and 2001, and 4 blocks in 2002. Contingency tables were used to examine the proportion of roads and powerlines present in monthly-ranges compared to non-range areas. The Breslow-Day test for homogeneity of odds ratios was used to test for a common odds ratios across months (Agresti 1996). Poisson rate regression was used to model the number of wells present in monthly-ranges as a function of use month and year. Backward selection was used to find the most parsimonious model that fit well, and model fit was assessed by examining the scale parameter (deviance / df) and residual plots.

Sagebrush density was estimated for monthly- and non-ranges of lesser prairie-chickens using the modification of the point-center quarter (PCQ) method described above. Density was estimated from a database of >3,000 points where PCQ measurements were taken. I tested for the effect of use on differences in density between ranges using a mixed model ANOVA, blocking on month.

Permutations of structure distance.—Because structures were not randomly or uniformly located on the landscape in relation to monthly-ranges, I used a modified Monte Carlo simulation (Manly 1997) to test whether the centroids of monthly-ranges were farther from structures than would be expected at random. If the structures had no impact on the birds' monthly-ranges, then one would expect the distances between these centroids and the structures to follow the same distribution as distances to randomly-placed points. If, on the other hand, the birds demonstrated some avoidance of these structures, as hypothesized, then the centroids closest to these structures should tend to be farther away than the random points. I therefore compared the 5th, 10th, 20th, 30th and 40th percentiles of the observed distances to the respective distributions of the corresponding percentiles from randomly-placed points as follows: 1) random resamples of 81 distances were taken from the distribution of 100,000 random points and distances; 2) this was repeated 1,000 times (thus generating 1,000 resamples of 81 distances); 3) the 5th, 10th, 20th, 30th and 40th percentiles for each resample were calculated; 4) an estimated sampling distribution of each percentile was created based on the 1000 calculated percentiles; and 5) the observed percentile distances were compared to the the upper tail of their respective sampling distribution. If the observed percentile distance was too extreme in the upper tail (i.e. in the upper 5% of the distribution), the H_0 (structures do not affect

monthly-range placements) was rejected. Support for the H_a , that structures have a negative impact on habitat use was then examined. The observed percentiles and the expected (mean) value of that percentile under randomness were compared.

RESULTS

Use and non-use

A total of 281 lesser prairie-chickens were captured and 160 (male = 76, female = 84) were fitted with transmitters. This resulted in 21,373 daily locations from 1997 to 1999. Vegetation sampling points in use ($n = 44$), non-use ($n = 38$), and absent ($n = 46$) areas were also used to calculate distances to landscape features. The MANOVA results indicated habitat selection by prairie chickens (Wilks $\Lambda = 0.352$, $F_{20,222} = 7.58$, $P < 0.0001$) with large numbers of multiple comparisons with effect sizes 1- to 2-fold differences between means (Table 1). The dimensionality of $H_a = 2$ (canonical variate-1, $F_{20,222} = 7.58$, $P < 0.0001$; canonical variate-2, $F_{9,112} = 2.48$, $P = 0.013$) and canonical variates-1 and -2 (CAN-1 and CAN-2) explained 87 and 13% of the data, respectively. Canonical variate-1 was positively correlated with sagebrush density, cover, and diameter (Table 1), but negatively correlated with distance to wells and structures; collectively this describes absent-sites. Canonical variate-2 had the strongest positive correlation with distance to powerline, and use-sites (Table 2). Thus, lesser prairie-chicken habitat use was generalized by the linear combinations, CAN-1 and CAN-2, of sagebrush stand characteristics and well proximity, and distance to powerlines, respectively. Effect sizes and 95% confidence intervals of the mean CAN-1 scores (Table 2) for use, non-use, and absent areas indicated that differences in shrub habitat were similar between use and non-use sites ($\bar{x}_{use} - \bar{x}_{non-use} = 0.365$, 95% CI: -0.070, 0.800), but differed markedly from

absent sites ($\bar{x}_{absent} - \bar{x}_{non-use} = 2.621$, 95% CI: 2.183, 3.059; $\bar{x}_{absent} - \bar{x}_{use} = 2.256$, 95% CI: 1.816, 2.696). This was supported by sagebrush density estimates obtained from calculations of all sampling points within each area. Densities were: absent = 7, 205 SE = 573; non-use = 2,553 SE = 201; and use sites = 3,144 SE = 249 ha⁻¹. Conversely, CAN-2 scores revealed (Table 2) greater similarity between non-use and absent sites in terms of distance to landscape features ($\bar{x}_{absent} - \bar{x}_{non-use} = 0.403$, 95% CI: -0.034, 0.841) than between either of these areas, and use sites ($\bar{x}_{use} - \bar{x}_{non-use} = 0.661$, 95% CI: 0.221, 1.101 $\bar{x}_{use} - \bar{x}_{absent} = 1.064$, 95% CI: 0.629, 1.499). Examination of the 2-dimensional plot and 95% confidence ellipses indicated complete separation between use, non-use, and absent sites (Fig. 1), along the sagebrush and landscape feature gradients.

Monthly-ranges

A total of 147 females were captured and fitted with radio transmitters from 2000 to 2002; only 95 birds provided enough data to be included in the analysis of 283 monthly-ranges (Table 3). The Breslow-Day test for the odds of roads occurring in monthly-ranges indicated that the odds ratios were significantly different across months in 2 of 3 years (2000 $\chi^2 = 28.62$, df = 5, $P < 0.0001$; 2001; $\chi^2 = 29.07$, df = 5, $P < 0.0001$; 2002; $\chi^2 = 80.58$, df = 3, $P < 0.0001$) for each year (Fig. 2). The odds of roads in a monthly-range were generally about 11% less than that of non-range sites. The Breslow-Day test for the odds of powerlines occurring in monthly-ranges indicated that the odds ratios varied throughout the sampling period (2000 $\chi^2 = 9.61$, df = 5, $P = 0.087$; 2001; $\chi^2 = 403.73$, df = 5, $P < 0.0001$; 2002; $\chi^2 = 21.52$, df = 3, $P < 0.0001$). The average odds of a powerline occurring in a monthly-range were 3 times ($n = 16$, SD = 0.28) less likely than in a non-range (Fig. 3). However, the odds increased in 2002 as

a number of birds had home ranges that overlapped with a newly constructed powerline. Sagebrush density was higher ($\bar{x}_{use} - \bar{x}_{non-use} = 817 \text{ ha}^{-1}$; $F_{1,18.6} = 63.28$, $P < 0.0001$) in monthly-ranges ($\bar{x} = 3,743$; $SE = 62.7 \text{ ha}^{-1}$) than areas outside of monthly-ranges ($\bar{x} = 2,996$; $SE = 62.7 \text{ ha}^{-1}$)

Backward selection of Poisson rate regression models of counts of wells as a function of prairie chicken use indicated that a model containing year \times month and month \times use interaction and all main effects was the best fit (deviance / df = 0.448). Estimates of the mean differences in number of wells per monthly-range varied by month (Fig. 4) with the months of April, July, and September having slightly fewer wells $\text{ha}^{-1,000}$ than non-range sites.

Monte Carlo simulations of distances to structures indicated that average monthly-centroids (O) were farther than expected at random (E) for the 5th ($E = 967 \text{ m}$; $O = 1,228 \text{ m}$; $P < 0.001$), 10th ($E = 1,241 \text{ m}$; $O = 1,403 \text{ m}$; $P < 0.001$), 20th ($E = 1,615 \text{ m}$; $O = 1,654 \text{ m}$; $P < 0.001$), 30th ($E = 1,759 \text{ m}$; $O = 1,785 \text{ m}$; $P < 0.05$), and 40th percentiles ($E = 1,998 \text{ m}$; $O = 2,006 \text{ m}$; $P < 0.05$).

DISCUSSION

This study is the first to document meso-scale factors that likely contribute to reduced suitability of lesser prairie-chicken habitat. The landscape features, proportion of an area occupied by powerlines and proximity to human structures, clearly reduced use of otherwise suitable habitat. This was evidenced by the greater distance between prairie chicken use sites and powerlines (1–2 fold difference), and the low odds ratios of powerline occurrence. Monte Carlo simulations indicated that the nearest 40% of lesser prairie-chicken centers of use were farther from anthropogenic features than would be

expected at random. However, the relationship of habitat usage as it pertains to sagebrush density and cover was less clear. Generally, it would appear that sagebrush densities in use areas were slightly higher on average than in non-use areas, but absent sites had larger shrubs and at higher estimated densities. This suggests that the habitat may otherwise be suitable, and further work is needed to discern these relationships. The other factors that were important to the absent area were the proximity of wells and structures as they were negatively related with CAN-1. Based on their mean distance values of 759 and 323 m, wells and structures were significantly closer to sampling points, respectively, on the absent site than either use or non-use sites. However, non-use sites were 336 m closer to structures than use sites. Combined, these data suggest that lesser prairie-chickens used areas with less anthropogenic disturbance.

Roads seemed to have little impact on prairie chicken habitat use, however the roads included here were of various quality: from paved 2-lane highways to unimproved 2-tracks through the sandhills. Pitman (2003) found that nesting female lesser prairie-chickens placed nest sites farther from paved roads than would be expected at random. Given the relatively large ranges ($\bar{x} = 326$ ha or 3.2 km^2) of female prairie chickens in this study it is not surprising that the proportion of roads was not significantly different across area types. Oyler-McCance (1999) modeled Gunnison sage-grouse (*Centrocercus minimus*) patch occupancy and found that the probability of patch occupancy was positively correlated with distance from a paved road. Patch occupancy was best described by landscape scale features when compared to models that included microhabitat parameters (Oyler-McCance 1999). The potential for landscape features to

reduce the suitability of microhabitat variables may be more widespread, as was indicated in my study.

Previous work indicated that changes in habitat composition at large scales (7,200 ha) explained most of the variability in declining lesser prairie-chicken populations (Woodward et al. 2001, Fuhlendorf et al. 2002). Fuhlendorf et al. (2002) did find that increased edge density was a significant factor in declining populations at the 3 smallest scales (405, 952, and 1810 ha) in their study, and they suggested that such changes have the greatest impacts on breeding activities. If such increased edge density was correlated to powerline, well, or structure density (in this study) and decreased reproductive output, then it could explain in part why the absent and non-use sites were less suitable for lesser prairie-chicken occupancy. Woodward et al. (2001) reported that population indices remained stable in landscapes where shrub cover was lost at a slower rate. While such losses have not occurred on these study areas in 15–20 years, the internal fragmentation and habitat loss (i.e., road and powerline construction) likely are contributing to the unsuitable portions of the study area.

Earlier work (Crawford and Bolen 1976, Taylor and Guthery 1980, Jamison 2000) described habitat use and suitability as it pertained primarily to the proportion of agriculture in a landscape. Crawford and Bolen (1976) suggested that when landscapes reach <63% native rangeland they are unsuitable habitat. Taylor and Guthery (1980) suggested that a minimum of 3.2 km² is needed to maintain prairie chickens. Although important, these studies failed to describe the necessary cover and other extrinsic factors within a fragment that make it suitable for prairie chickens.

MANAGEMENT IMPLICATIONS

Future impact assessments should consider the construction of new anthropogenic features as a potential detriment to habitat suitability for lesser prairie-chickens.

Conservation planning and habitat inventory should carefully consider the proximity and density of anthropogenic features when prioritizing habitat patches for conservation action or mitigation. Further work is needed to clarify the potential interaction between sagebrush stand characteristics (density and plant morphology) and landscape features as it pertains to habitat suitability. Future research should examine how the quantities (or proximity) of anthropogenic features affect the probability of patch occupancy across replicate sites of various sizes and levels of disturbance.

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Table 1. Parameter estimates of habitat and landscape features for lesser prairie-chicken use, non-use and absent sites. Means and standard errors are presented for measured variables along with the standardized canonical scores (CAN-1 and CAN-2) for each variable. Columns with different letters indicate a significant difference ($P < 0.05$).

Variable	Area type			Standardized canonical scores	
	Use	Non-use	Absent	CAN-1	CAN-2
Shrub cover (%)	15.3 \pm 3.1A	13.6 \pm 3.1A	35.0 \pm 3.1B	0.428	-0.559
Forb cover (%)	9.7 \pm 1.4A	7.7 \pm 1.4A	8.9 \pm 1.5A	0.441	0.015
Grass cover (%)	13.4 \pm 1.7A	14.3 \pm 1.6A	14.1 \pm 1.7A	-0.360	-0.521
Litter cover (%)	29.9 \pm 2.4A	38.6 \pm 2.4B	16.4 \pm 2.5C	0.248	0.028
Shrub density (m ²)	2.5 \pm 0.2A	2.0 \pm 0.2A	4.4 \pm 0.2B	0.870	0.290
Shrub diam (cm)	71.0 \pm 3.2A	67.7 \pm 3.1A	80.1 \pm 3.3B	0.217	-0.213
Distances (m)					
Wells	435.0 \pm 31.2A	446.0 \pm 30.8A	323.2 \pm 31.6B	-0.382	0.104
Roads	193.2 \pm 18.7A	178.8 \pm 18.6A	184.4 \pm 19.0A	-0.071	0.114
Structure	1,397 \pm 106A	1,061 \pm 105B	759 \pm 108C	-0.332	-0.040
Powerlines	1,106 \pm 81A	666 \pm 80B	705 \pm 82B	-0.060	1.024

Table 2. Canonical scores and sagebrush density plants ha⁻¹ ($\bar{x} \pm \text{SE}$) of lesser prairie-chicken use area type. Differences in usage area type are defined in the text.

Variate/ sagebrush	Area type		
	Use	Non-use	Absent
CAN-1	-0.561 ± 0.158	-0.926 ± 0.154	1.694 ± 0.158
CAN-2	0.591 ± 0.158	-0.472 ± 0.154	-0.069 ± 0.158
Sagebrush density ha ⁻¹	$3,144 \pm 249$	$2,553 \pm 201$	$7,205 \pm 573$

Table 3. Count data of landscape features for contingency table and Poisson rate regression modeling of lesser prairie-chicken monthly-ranges.

Year	Apr	May	Jun	Jul	Aug	Sep
2000						
No. ranges	30	8	21	23	17	17
Avg. ha	553	667	273	170	148	180
Points in ranges	111,493	72,929	5,258	33,076	35,084	3,561
Roads (points)	2,597	1,575	1,127	617	829	752
Powerlines (points)	150	58	37	26	38	27
No. wells	52	44	21	10	13	8
2001						
No. ranges	15	9	18	24	25	23
Avg. ha	805	1045	396	182	119	151
Points in ranges	97,064	107,238	78,575	42,787	41,272	34,033
Roads (points)	2233	2522	2025	1024	951	763
Powerlines (points)	144	213	398	54	38	60
No. wells	44	58	39	17	19	13
2002						
No. ranges	11	8	16	16	ND	ND
Avg. ha	584	231	306	135	ND	ND
Points in ranges	61,526	27,107	64,288	30,491	ND	ND
Roads (points)	1,729	600	1,420	672	ND	ND
Powerlines (points)	540	241	518	186	ND	ND
No. wells	24	12	34	10	ND	ND

Fig 1. Mean canonical variates (CAN-1 and CAN-2), SEs (in both x,y) and their respective 95 % confidence circles for lesser prairie-chicken use, non-use and absent sites. CAN-1 was best explained by high sagebrush densities and large shrubs. Distances to structures and wells also explained CAN-1, but were negatively related. This revealed that that absent sites were in closer proximity to these anthropogenic features than other sites. CAN-2 was best explained by distance to powerlines. Although these sites separated in a 2-dimensional space, use and non-use did not differ in regards to their mean value of CAN-1, but both differed from the mean CAN-1 score of absent sites. Alternatively, non-use and absent sites were similar with respect to CAN-2 but differed from use sites, suggesting that distance to powerlines was important in determining suitability of lesser prairie-chicken habitat.

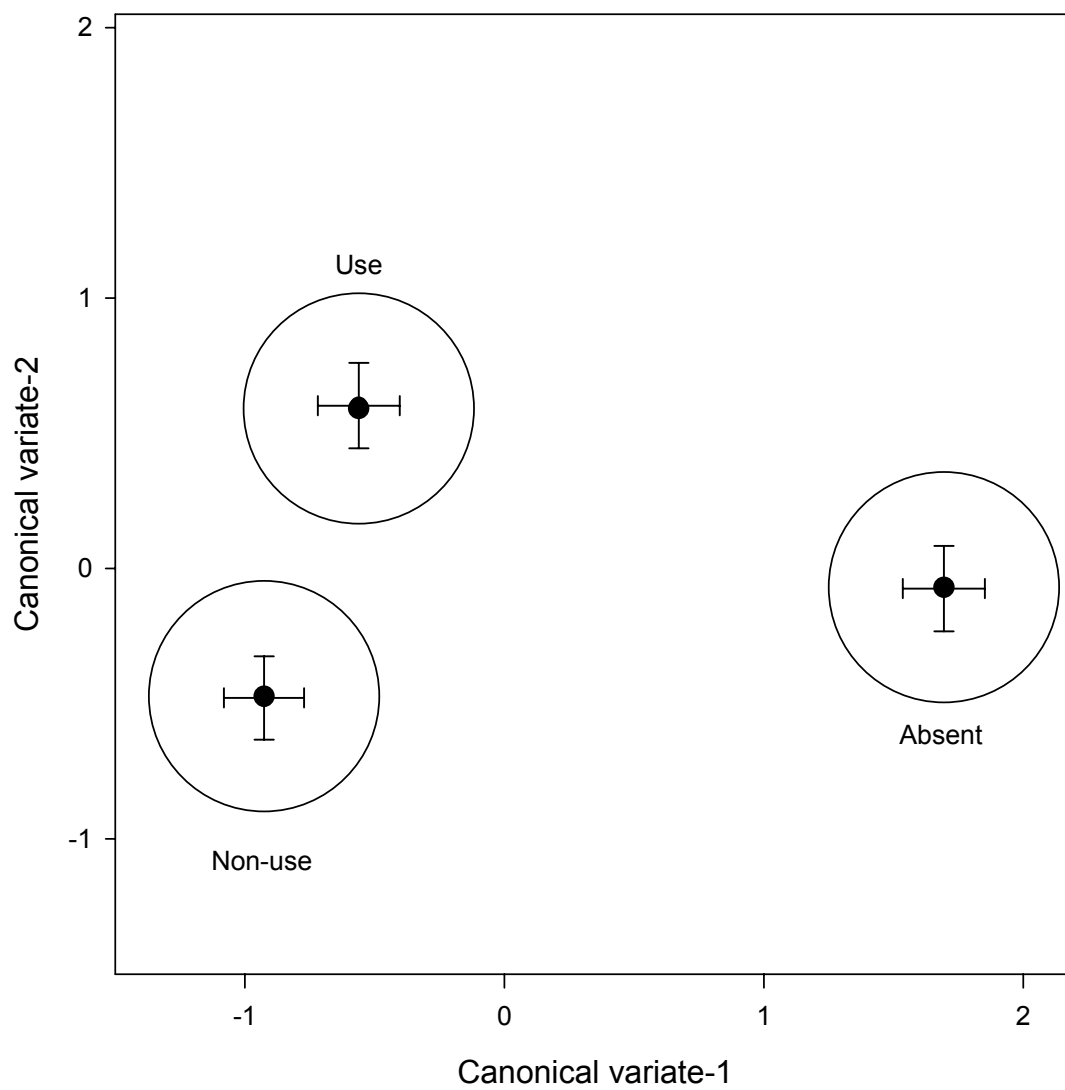


Fig. 2. Odds ratios (95% confidence limits) for roads occurring in lesser prairie-chicken monthly-ranges in 2000 (A), 2001 (B), and 2002 (C). The dashed line indicates odds of 1 and confidence limits intersecting this line indicate odds not different than expected by chance.

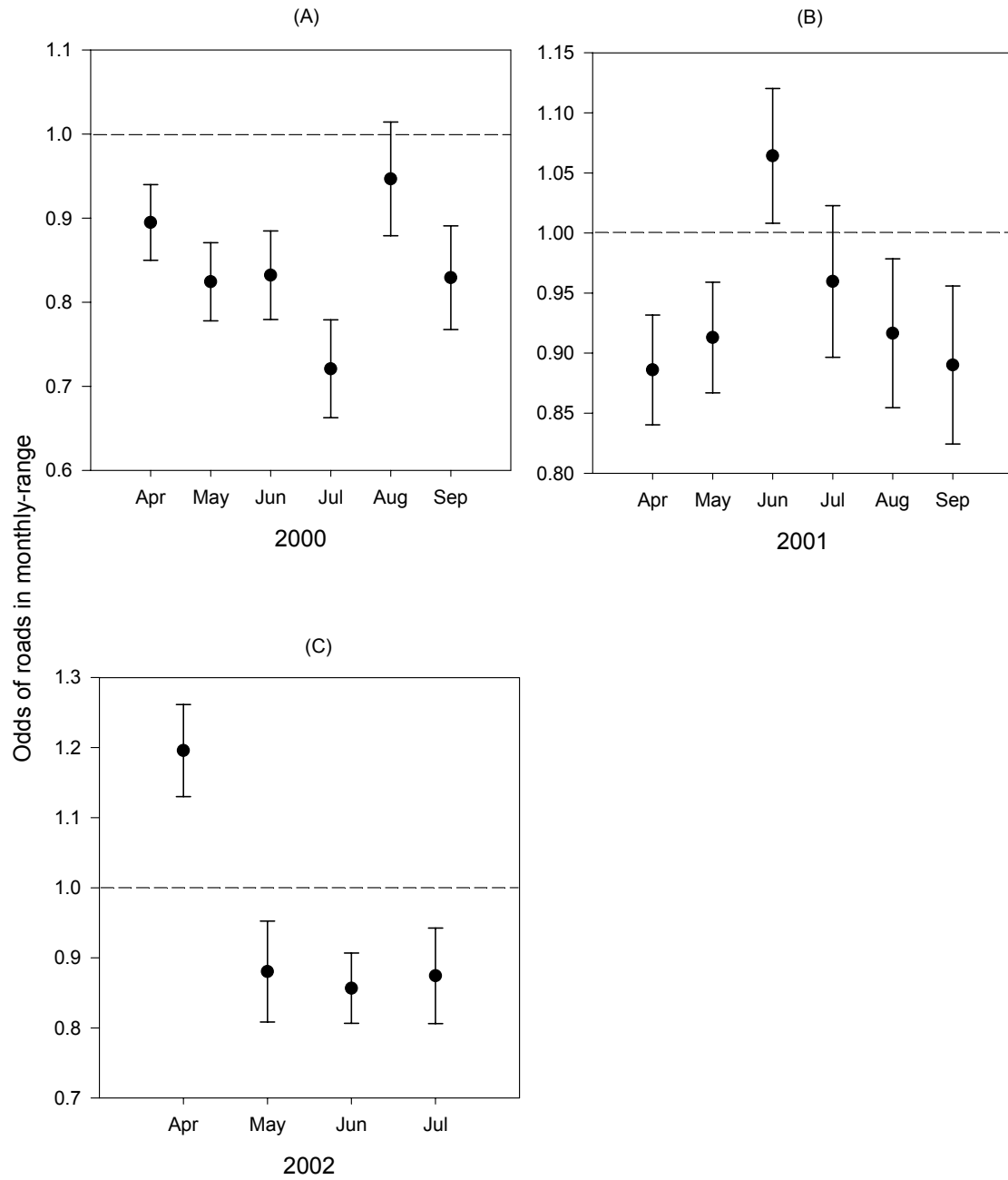


Fig. 3. Odds ratios (95% confidence limits) for powerlines occurring in lesser prairie-chicken monthly-ranges in 2000 (A), 2001 (B), and 2002 (C). The dashed line indicates odds of 1 and confidence limits intersecting this line indicate odds not different than expected by chance.

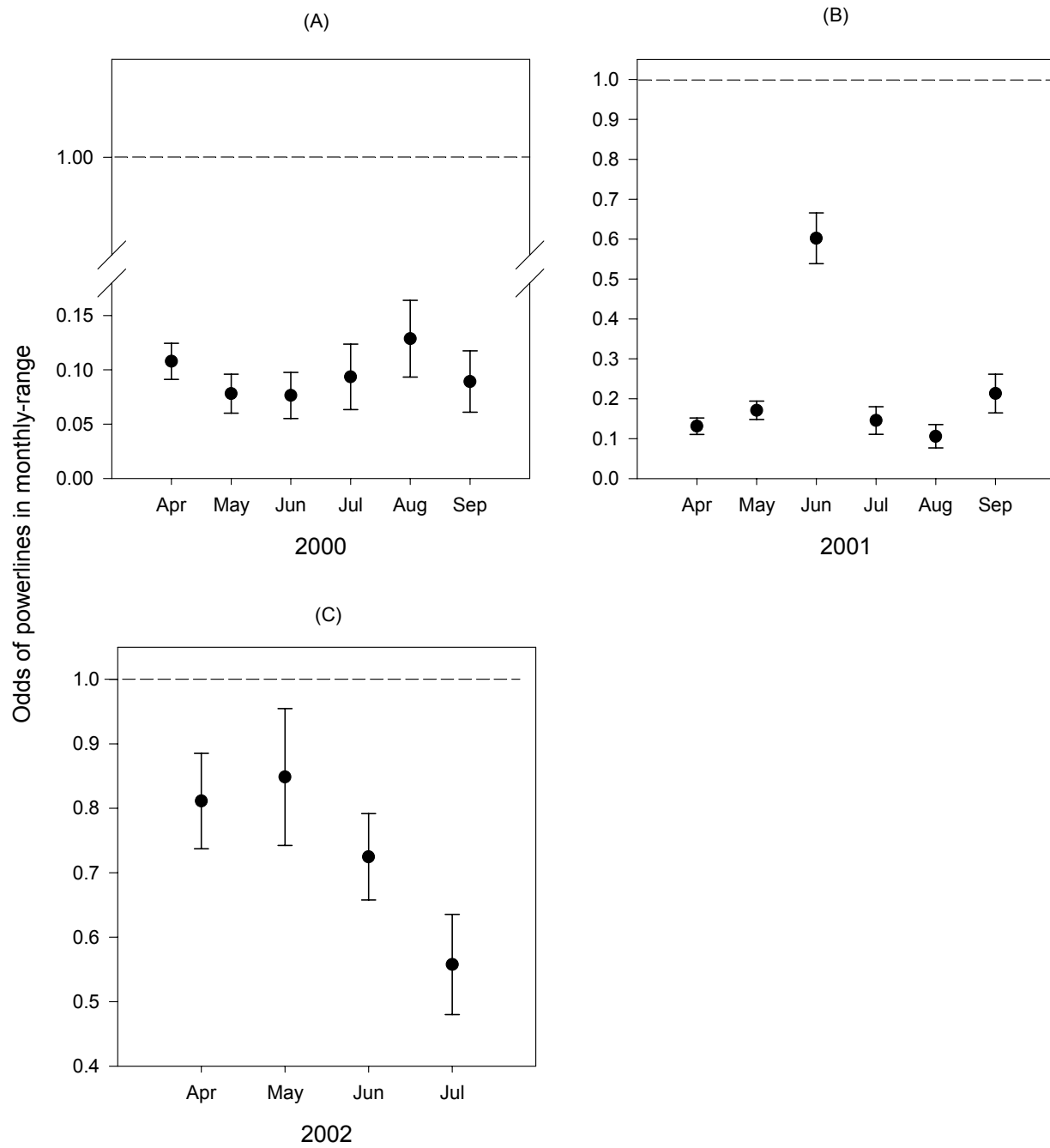
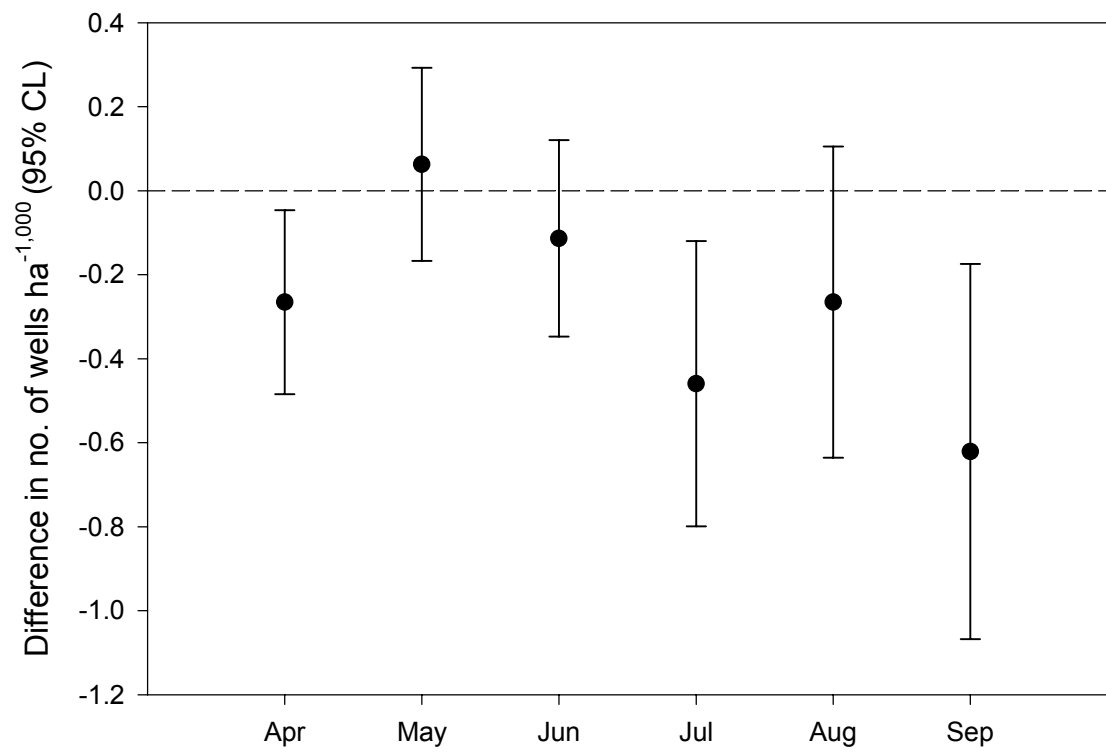


Fig. 4. Differences in the mean number (95% confidence limits) of wells $\text{ha}^{-1,000}$ between monthly- and non-ranges as determined from Poisson rate regression. The dashed line indicates a difference of 0 and confidence limits intersecting this line indicate a observed values did not differ from those expected by chance.



OVERALL STUDY SUMMARY

Introduction

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) has sustained marked reductions in suitable habitat over the past 100 years. The remaining habitat is widely used for petroleum exploration and extraction, cattle grazing, powerline easements, and the generation of electricity. It is estimated that over 90% of the range has been lost since the turn of the 20th century and the range wide population has paralleled these losses. In 1995, the lesser prairie-chicken was petitioned to be listed as threatened under the Endangered Species Act. Given the status of this sensitive species it is critical to understand the dynamics of local and regional populations and possible management scenarios that would most effectively benefit the lesser prairie-chicken.

This study is the culmination of two Federal Aid in Wildlife Restoration projects, W-47-R and W-53-R. Field work for W-47-R began in spring 1997 and was completed in November 1999, and W-53-R was initiated in December 1999 and concluded in March 2003. Project W-47-R was located on a 5,700-ha fragment of sand sagebrush prairie (Area I) south of the Arkansas River (~ 4 km south of Holcomb, Finney County, Kansas). Project W-53-R added second study site (Area II) of 5,400 ha. The center of Area II was ~20 km east of Area I. Research was conducted simultaneously on both sites from spring 2000 through spring 2003. Primary research objectives were to gather information on specific demographic parameters and examine population viability and sensitivity to changes in the parameters.

A total of 755 lesser prairie-chickens were captured and banded from 1997 to 2002, and 136 male (46 yearling, 66 adult, 24 age undetermined), and 227 female (87 yearling, 117 adult, and 23 age undetermined) were fitted with radio transmitters. Radiomarked birds were tracked daily using vehicle mounted antennae, resulting in 39,969 daily bird locations. These data were used to determine nest success, chick survival, adult survivorship, habitat usage, and the resulting parameter estimates were used as inputs to the demographic model.

Age-specific survival of males

Robust estimates of annual survival are useful for two reasons: understanding management efforts and basic science. Survival is one of several demographic rates that can effect the fluctuations in population numbers of grouse and the occurrence of age-specific survival and reproductive rates may covary with the type of mating system in grouse. Three hundred and seventy-six male prairie-chickens (173 yearlings, 203 adults) were captured from 1998-2002, and 150 males (78 yearlings, 72 adults) were recaptured at least once. Analyses of live mark-recapture data were used to estimate survival. Local survival rates (ϕ) of male lesser prairie-chickens were highest for yearling ($\phi^1 = 0.615$) > adult ($\phi^1 = 0.485$) > older adults ($\phi^2 = 0.347$). Twenty percent of recaptured yearlings switched leks in their second year, and were 2.5 (odds ratio) times as likely than adults to do so (8%). Each age-class was equally likely (~17.5 %) to move between leks within a breeding season. Four and 15 % of yearlings and adults were recaptured > 3 times, respectively. This suggests that adults had a greater propensity to attend leks and presumably try to obtain copulations than yearlings. The overall estimates of lesser

prairie-chicken survival were slightly elevated when compared to that of other banding studies of prairie grouse.

Effects of radiomarking on lesser prairie-chicken survival

Radiotelemetry has provided wildlife biologists a tool to estimate survival where fate of each individual is likely known. While these analyses of these data can result in highly accurate estimates, five assumptions must be met. Two of the assumptions, random right-censoring and no-transmitter effect on survival, are often difficult to assess in studies. Male lesser prairie-chickens in this study were not measurably impacted by radiomarking, as their survival rates were greater than or equal to those of banded birds. The model best supported by the data, $S_c, p_{group+t}, r_g, Fc$, indicated that survival was best modeled as constant ($\hat{S}_c = 0.731$, SE = 0.072) across radiomarked and banded birds. Signal loss occurred throughout the monitoring period and appeared to be independent of periods of high mortality. Eight of 16 (50%) right-censored birds were subsequently recaptured, which was similar to the recapture rates for known-fate birds (55.8%), suggesting that right-censored birds had similar survival rates to that of known-fate individuals.

Survival of male and female lesser prairie-chickens

In total, 136 male (46 yearling, 66 adult, 24 age undetermined), and 227 female (87 yearling, 117 adult, and 23 age undetermined) lesser prairie-chickens were captured and fitted with radio transmitters. Year to year variation in summer survival was evident and seemed to be highly related to mortality rates of incubating females on nests and >30% of all female mortality was associated with the nesting period. Summer survival rates (Apr-Nov) and apparent nest success from 5 years revealed the strength of this

relationship. Gender-specific survival was not well supported by the data, as the overall survival rates of males and females were similar in the summer ($S_{\text{male}} = 0.69$; $S_{\text{female}} = 0.67$) and seasonal (Apr-Mar) analyses ($S_{\text{male}} = 0.39$; $S_{\text{female}} = 0.43$). However, the timing of survival over 12-months suggested that seasonal patterns in male survivorship do not match the temporal pattern seen in females.

Age-specific patterns in female survival were evident in both analyses with yearling birds ($S_{\text{summer}} = 0.75$; $S_{\text{seasonal}} = 0.52$), surviving at a higher rate than adults ($S_{\text{summer}} = 0.69$, $S_{\text{seasonal}} = 0.37$). One explanation for this difference is the cost of reproduction, as it may result in reduced survival rates of adults, if they had higher reproductive output, but, reproductive parameters were similar between age-classes in this study. Management of lesser prairie-chickens should focus on habitat manipulations that increase nest survival and decrease female losses during incubation. In fragmented populations, predator control may achieve short-term goals of increased female survival and nest success, but may be too costly to sustain in the long-term

Probable causes of mortality

One-hundred and thirty four mortalities were recorded from spring 1997 to spring 2003, and the majority of mortality was attributed to mammalian predation (54%). Males seemed more susceptible to raptor predation (20%) than females (11%) but were not measurably different. Seven of the eight accidents were associated with powerline collisions. Losses to recreational hunting were small (5%) relative to the radiotelemetry population, but even less (1.2%) when compared to banded birds that were available for harvesting. Males apparently were more susceptible to hunting losses than females.

Demographic model

The arithmetic rate of population change (λ) for each population projected 25-46% declines, but only Area I was significantly different from $\lambda = 1$. Age-ratios (0.27-0.786 yearling/adult) during spring trapping suggested either recruitment from outside the study area or a negative bias in estimated rates of reproduction was contributing to this observed rate. These contributions derived from retrospective analysis were several orders of magnitude larger in the case of nest success but less so for chick survival indicating that differences in these rates were determining the variation in λ for these populations. The importance of post-brood survival to these populations may be two-fold: 1) it is an index to the limitations of the actual recruitment rate, and 2) if the observed λ 's do indicate declining populations, then post-brood survival may also reflect the sensitivity of λ to immigration from other habitat patches. Ascertaining the viability of these populations was difficult given that both sampling and process variance were included in the parameter estimates. However, efforts to increase nesting success and chick survival are paramount, and the former likely will increase female survival. The tenuous stability of λ in these two populations suggests that these fragmented populations are maintained in part by immigration.

Habitat usage and anthropogenic features

Landscape features, proportion of an area in powerlines, and proximity to human structures, were clearly associated with habitat suitability. This was evidenced by the greater distance between prairie chicken use sites and powerlines (1-2 fold difference), and the low odds ratios of poweline occurrence. Based on their mean distance values of

759 and 323 m, structures and wells were significantly closer to sampling points, respectively, on the absent site than either use or non-use sites. However, non-use sites were 336 m closer to structures than use sites. Monte Carlo simulations indicated that $\geq 60\%$ of lesser prairie-chicken centers of use were further from anthropogenic features than would be expected at random. Combined, these data suggest that lesser prairie-chickens used areas with less anthropogenic disturbance.

The relationship of habitat usage as it pertains to sagebrush density and cover may be non-linear. Future impact assessments and conservation plans should consider the construction or presence of anthropogenic features as a potential detriment to habitat suitability for lesser prairie-chickens. Habitat inventories should carefully consider the proximity and density of anthropogenic features when prioritizing habitat patches for conservation action or mitigation. Further work is needed to clarify the potential non-linear relationship between habitat suitability and sagebrush stand characteristics.

APPENDIX I

A RANGE-WIDE GENETIC EVALUATION OF LESSER PRAIRIE-CHICKENS

INTRODUCTION

The current distribution of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) is highly fragmented throughout the species' range, and its habitat is widely used for agriculture, housing developments, petroleum exploration and extraction, cattle grazing, power line easements, and the generation of electricity. The cumulative loss of habitat and declining population trends led to the "warranted but precluded" threatened listing under the Endangered Species Act (U.S. Fish and Wildlife Service 2002).

It has been hypothesized that genetic factors may be contributing to the observed population trends. Such was the case for remnant greater prairie-chicken (*T. cupido*) populations in Illinois and Wisconsin that sustained a population bottleneck (Bouzat et al. 1998, Bellinger et al. 2003). The demographic and genetic consequences were reduced fertility and heterozygosity, respectively (Bouzat et al. 1998). Could similar processes be at work with the lesser prairie-chicken when populations have been substantially reduced? Van Den Bussche et al. (2003) found reasonable levels of heterozygosity (both in mitochondrial DNA and in the nuclear genome) of lesser prairie-chickens in Oklahoma and New Mexico, suggesting that genetic variation is not limiting to population growth. This paper expands on Van Den Bussche et al. (2003) and includes 4 populations from Kansas and 1 from southeastern Colorado. Mitochondrial DNA (mtDNA) was evaluated for all populations but microsatellites were only assessed for 2 fragments of sand

sagebrush (*Artemisia filifolia*) prairie in Finney County (Finney-1 and Finney-2) and 1 in Kearny County, Kansas at the time of this report.

METHODS

Study areas

Populations were from 6 counties in Kansas (Fig. 1), 3 north (Gove, Trego, and Ness) and 3 south (Comanche, Finney, Kearny) of the Arkansas River. Populations in Baca and Prowers counties Colorado were also sampled. Because of small sample sizes and genetic similarities Baca and Prowers, and Gove, Trego, and Ness counties were pooled into 2 populations and referred to as Colorado and Gove, respectively. Range-wide comparisons of mtDNA were made to populations previously described in Van den Bussche et al. (2003). Comparisons were made on the county level instead of a lek-by-lek level, and included Harper (pooling Harper and Ellis) and Beaver, Oklahoma, and Roosevelt, New Mexico (hereafter New Mexico). The methods below refer only to the sampling conducted between 2000 and 2002, although protocols for sequencing mtDNA were in place to ensure consistency with Van den Bussche et al. (2003).

Tissue collection

Blood samples were obtained from lesser prairie-chickens ($n = 127$) captured in funnel traps during the spring and fall (2000-02) (Haukos et al. 1991). Blood samples were obtained by clipping a toenail of each lesser prairie-chicken and placing 2–3 drops of blood into a microfuge tube previously coated with EDTA. All blood samples were frozen at -20°C .

DNA extraction and mtDNA sequencing

DNA was extracted from muscle tissue using either a phenol-chloroform method

(Kahn et al. 1999) or the Wizard Genomic DNA Purification System (Promega) following the manufacturer's instructions, except that 478 base pairs were examined. Sequences were aligned using Gene Tool Lite 1.0 (Double Twist Inc.), and each unique sequence was assigned a different haplotype designation.

Microsatellite genotype scoring

To evaluate finer scaled population structuring, variation in the nuclear genome was assessed by genotyping microsatellite loci of the 3 populations from which there were field data to compare movement rates (2 from Finney and 1 from Kearny County). Six primers for microsatellite loci (ADL23, ADL42, ADL44, ADL146, ADL162, ADL230) originally isolated from domestic chicken (*Gallus gallus*) and shown to be variable in greater prairie-chicken (*Tympanuchus cupido*; Bouzat et al. 1998), and 4 loci (SGCA5, SGCA9, SGCA11) developed for sage-grouse (*Centrocercus* spp.; Taylor et al. 2003), and 1(LLST1) developed for red grouse (*Lagopus lagopus scoticus*; Piertney et al. 1999) were used to evaluate genetic variability within the nuclear genome. The extraction and microsatellite scoring follows Taylor et al. (2003). A standard 25 µl PCR (Quinn 1992) was performed for each locus (MJ Research PTC-200) using a dye-labeled forward primer and an unlabeled reverse primer. The temperatures and times of the profiles were as follows: denaturation, 95°C for 1 minute; annealing, 60°C for 1 minute; extension, 72°C for 1 minute. Each PCR had 35 amplification cycles. A touch-down thermal profile was performed with all loci as follows: 1) pre-heat, 94°C for 1 minute; 2) denaturation, 92°C for 5 seconds; annealing, 66°C to 56°C (-0.5°C per cycle) for 30 seconds; 3) denaturation, 92°C for 5 seconds; annealing, 55°C for 30 seconds (+1 second per cycle); 4) final extension, 72°C for 10 minutes. Each denaturation and annealing

combination (2 and 3) cycled 20 times before the next step so that a total of 40 cycles were performed. Samples were run on the CEQ2000 XL DNA Analysis System (Beckman-Coulter). The SGCA11 samples were run with the S600 size standard using the Frag 4 default method. All other loci were run with the S400 standard and the Frag 3 default method.

Data Analyses

Mitochondrial DNA.—Estimates of haplotype (h) and nucleotide (π) diversity within populations were calculated in ARLEQUIN 2.0 (Schneider et al. 2000). Analysis of molecular variance (AMOVA) was used to quantify haplotype diversity at 3 different levels of a hierarchy. State and geographic regions (i.e., sand sagebrush prairie of Kansas and Colorado: Finney, Kearny, and Prowers; mixed-grass prairie of Kansas: Gove; mixed-shrub of Kansas: Comanche; mixed shrub of Oklahoma: Beaver and Harper; and sand shinnery oak [*Quercus havardii*] of New Mexico) was 1 level, the variation among populations within a region was the second level, and variation among individuals within populations as the third level. Population subdivision was examined in ARLEQUIN 2.0 (Schneider et al. 2000) using significance tests of pairwise population F_{ST} values. An F -test was calculated to determine whether the distribution of haplotypes among populations differed. The molecular distances between haplotypes was calculated using Nei's unbiased minimum distance (Nei 1978), and neighbor-joining trees were constructed showing the relationships among the 8 populations.

Microsatellites.—Allele frequencies, mean number of alleles per locus, deviations from Hardy-Weinberg expectation, and population differentiation were quantified in ARLEQUIN 2.0 (Schneider et al. 2000). Each locus at each population was tested for

deviations from Hardy-Weinberg expectations and $P < 0.05$ was the criterion for statistical significance. AMOVA and pairwise R_{ST} statistics were used to examine variation among populations and population subdivision, respectively.

RESULTS

Two-hundred and ninety-three lesser prairie-chickens were captured in Kansas and Colorado between 2000 and 2002: Finney-1 = 90, Finney-2 = 93, Kearny = 28, Comanche = 17, Gove = 45, and Colorado = 20. Due to logistics DNA was extracted from a sub-sample of birds from Finney-1 and -2, resulting in 127 samples for Kansas and Colorado.

Mitochondrial DNA

There were 45 different haplotypes across all individuals from both studies ($n = 278$), 31 of which had been previously described in Van den Bussche et al. (2003). Haplotypes A, B, C, and J were the most common haplotypes and each occurred in 5 to 8 of the populations (Fig. 2). Twenty-two unique haplotypes were found; Gove (7), Harper (7), New Mexico (3), Kearny (2), Beaver (2), and Comanche (1).

Within-population haplotype diversity (h), which represents the number and frequency of haplotypes was generally high for all populations, but New Mexico had the lowest (83%). Moderate levels of nucleotide diversity (π) were present in most populations, but again New Mexico had the lowest (0.7%). Genetic diversity attributable to variation within populations, among populations within regions, and between regions was partitioned as 94.2%, 1.4%, and 4.4%, respectively. Pairwise F_{ST} tests indicated substantial population differentiation (Table 2). New Mexico was statistically different

from all other populations, Finney, Beaver, and Gove were statistically different from most other populations.

Neighbor-joining tree analysis (Fig. 3) reflected the differences observed in the pairwise comparisons, and found substantial population structure among the 8 populations that is consistent with 4 geographic subdivisions of the populations: Kansas (Finney, Kearny [south of Arkansas River]) and Colorado; Kansas (Gove [north of Arkansas River]); Oklahoma (Beaver, Harper) and Kansas (Comanche[south of Arkansas River]); and New Mexico.

Microsatellites

All individuals ($n = 94$) from Finney-1, Finney-2, and Kearny were examined for 8 microsatellite loci, because of difficulties in scoring LLST1, it was removed from all analyses. SGCA11 had a significant departure from Hardy-Weinberg equilibrium for Finney-1 ($P = 0.011$) and Finney-2 ($P = 0.014$) and was not considered in further analyses. Additionally SGCA9 had 21 alleles which was > 2 -fold of any other loci, thus it was not included in further analyses. Several alleles were found at each of the remaining 5 loci and all were polymorphic (Table 3). The proportions of genetic diversity were partitioned as 77.4% within and 22.6% between populations. An exact test of population differentiation based initially on pairwise R_{ST} statistics found significant differentiation between Finney-1 and Kearny ($P = 0.011$), Finney-2 and Kearny ($P = 0.013$), but not between Finney-1 and Finney-2 ($P = 0.377$).

DISCUSSION

These lesser prairie-chicken populations were found to have relatively high levels of genetic diversity as was indicated by average heterozygosity and number of haplotypes

found within and among populations. However, the large number of base-pairs (478) examined in this study contributed to the large number of haplotype designations. A transversion analysis (that redefines haplotypes based on the rarity of a base-pair switch) may yield additional insights to population structuring. Birds from New Mexico had the fewest haplotypes, and were markedly different from other populations as evidenced by pairwise F_{ST} and neighbor-joining tree analyses. This suggests that this lesser prairie-chicken population has been isolated from the populations in the northeastern range. Although there was lower genetic diversity in this population, no deleterious effects to demographic rates have been documented (D. H. Wolfe, Sutton Research Center, unpublished data).

Pairwise F_{ST} tests ($P < 0.002$) indicated substantial population structuring among the 8 populations, and was consistent with geographic subdivision of populations: Kansas (Finney, Kearny[south of Arkansas River]) and Colorado; Kansas (Gove [north of Arkansas River]); Oklahoma (Beaver, Harper) and Kansas (Comanche[south of Arkansas River]); and New Mexico. This genetic and geographic structure suggests that birds north of the Arkansas River in Kansas have been separate from birds south of the River for many years, however, time since divergence has not been calculated. The geographic structuring of mtDNA appears to follow the general habitat types, sand sagebrush prairie of Kansas and Colorado, mixed-grass prairie of Kansas, mixed-shrub of Kansas and Oklahoma, and sand shinnery oak of New Mexico, which is probably an artifact of habitat fragmentation at a larger scale, but also could reflect genotypes adapted for these regional environmental gradients.

Microsatellite analyses of adult males from the Finney and Kearny populations indicated that male genetic structuring may be more pronounced at fine scales than was realized by the mtDNA analyses. Such localized genetic flow of males is logical given that juvenile males generally do not disperse >2 km from their natal site (Pitman 2003). Alternatively, the mtDNA analyses included females and indicated no differentiation between these populations indicating that females likely are responsible for most of the genetic diversity across these populations. This was evidenced in part by radiotelemetry studies from Finney County that indicated a 20% emigration rate (Chapter 3) of all radiomarked birds (only 2 were males), and these birds moved between 20 and 50 km from the county to other sagebrush fragments.

Studies of greater prairie-chicken genetics have found reduced numbers of alleles in contemporary populations (7) compared to those of historic populations (9.2) (Bellinger et al. 2003). Bouzat et al. (1998) documented >5 alleles in all populations except Illinois, which had 3.7 alleles per locus. Van den Bussche et al. (2003) reported 5.8 and 4.8 alleles per locus in Oklahoma and New Mexico lesser prairie-chicken populations, respectively, that had > 20 samples. This was comparable to the number of alleles found in this study 4.8–5.0. What is less clear is the relationship of these allelic frequencies compared to historic samples.

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Table 1. Descriptive statistics based on DNA sequence data of a portion of the mtDNA D-loop for 8 lesser prairie-chicken populations.

Population location	mtDNA statistics ^a			
	<i>n</i>	A	<i>h</i> (SE)	π (SE)
Finney, KS	35	14	0.919 (0.021)	0.014 (0.008)
Kearny, KS	24	12	0.909 (0.038)	0.080 (0.040)
Gove, KS	39	20	0.947 (0.020)	0.012 (0.007)
Comanche, KS	14	9	0.912 (0.059)	0.069 (0.036)
Beaver, OK	27	12	0.912 (0.028)	0.012 (0.007)
Harper, OK	61	23	0.944 (0.012)	0.014 (0.007)
Prowers, CO	15	10	0.952 (0.034)	0.012 (0.007)
Roosevelt, NM	63	9	0.828 (0.027)	0.007 (0.004)

^a *n* = sample size, *A* = number of haplotypes, *h* = haplotype diversity, and π = nucleotide diversity.

Table 2. Significance ($P < 0.0017$) of pairwise F_{ST} tests for mtDNA sequencing data from 8 populations of lesser prairie-chickens in 4 states. Pairs of populations significantly different are shown by + and those not significantly different are shown by –.

Population location	Population						
	Finney	Kearny	Gove	Coman	Beaver	Harper	Colo.
				-che			
Kearny, KS	–						
Gove, KS	+	+					
Comanche, KS	+	–	–				
Beaver, OK	+	+	+	–			
Harper, OK	+	–	+	–	–		
Prowers, CO	–	–	–	–	+	–	
Roosevelt, NM	+	+	+	+	+	+	+

Table 3. Number of alleles and average expected and observed heterozygosity at 5 microsatellite loci for 3 populations of lesser prairie-chickens in southwestern Kansas.

Population location	Microsatellite statistics ^a			
	<i>n</i>	A	H_O (SD)	H_E (SD)
Finney-1, KS	32	4.8	0.453 (0.121)	0.505 (0.132)
Finney-2, KS	35	5.0	0.530 (0.116)	0.550 (0.116)
Kearny, KS	27	4.8	0.451 (0.079)	0.536 (0.094)

^a n = sample size, A = average number of alleles, H_O = mean observed heterozygosity, and H_E = mean expected heterozygosity under Hardy-Weinberg equilibrium.

Fig. 1. Sampling locations (black dots) and counties (gray polygons) of lesser prairie-chickens for genetic evaluations. Rivers indicated by black irregular lines. Oklahoma and New Mexico sites are from Van den Bussche et al. (2003).

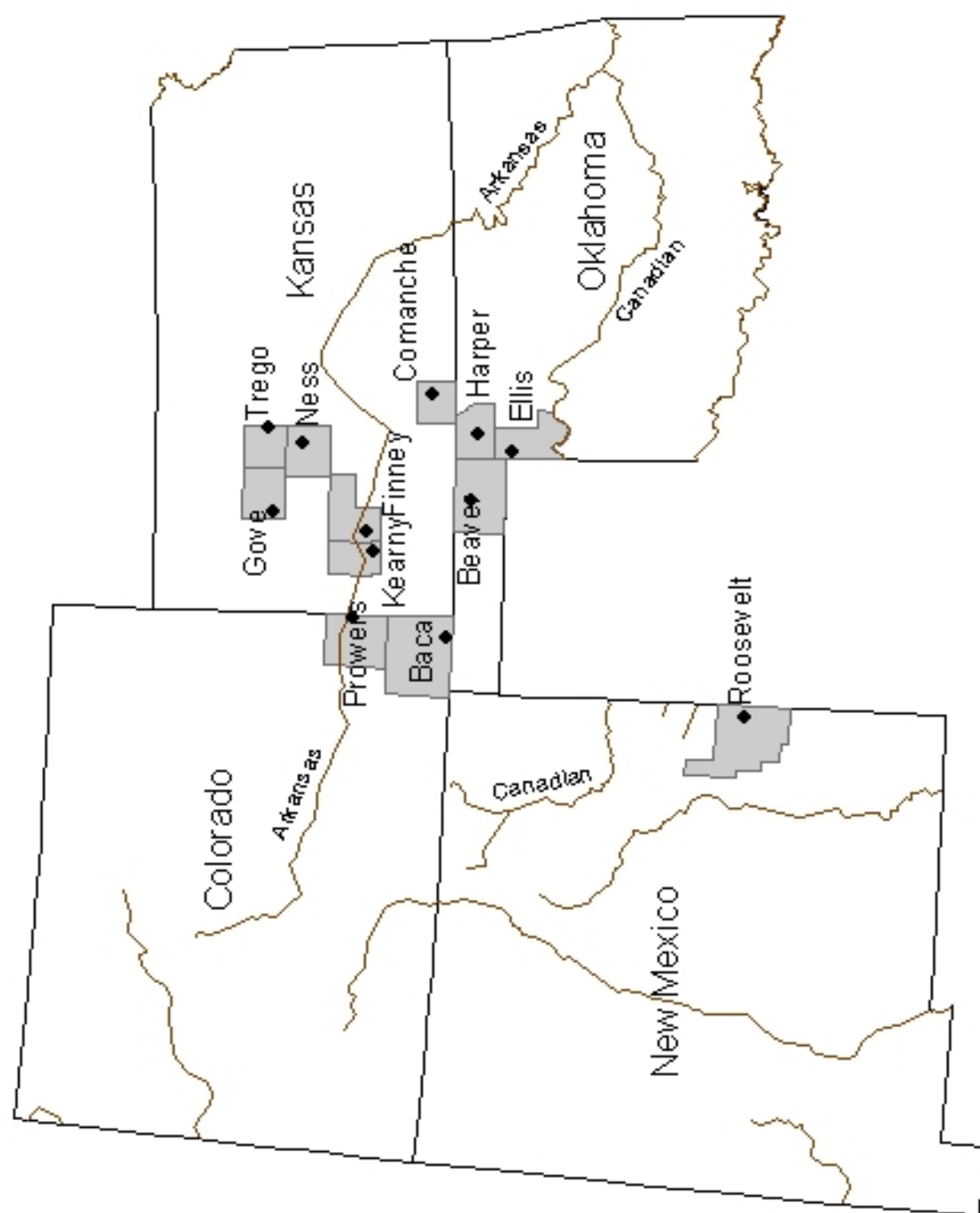
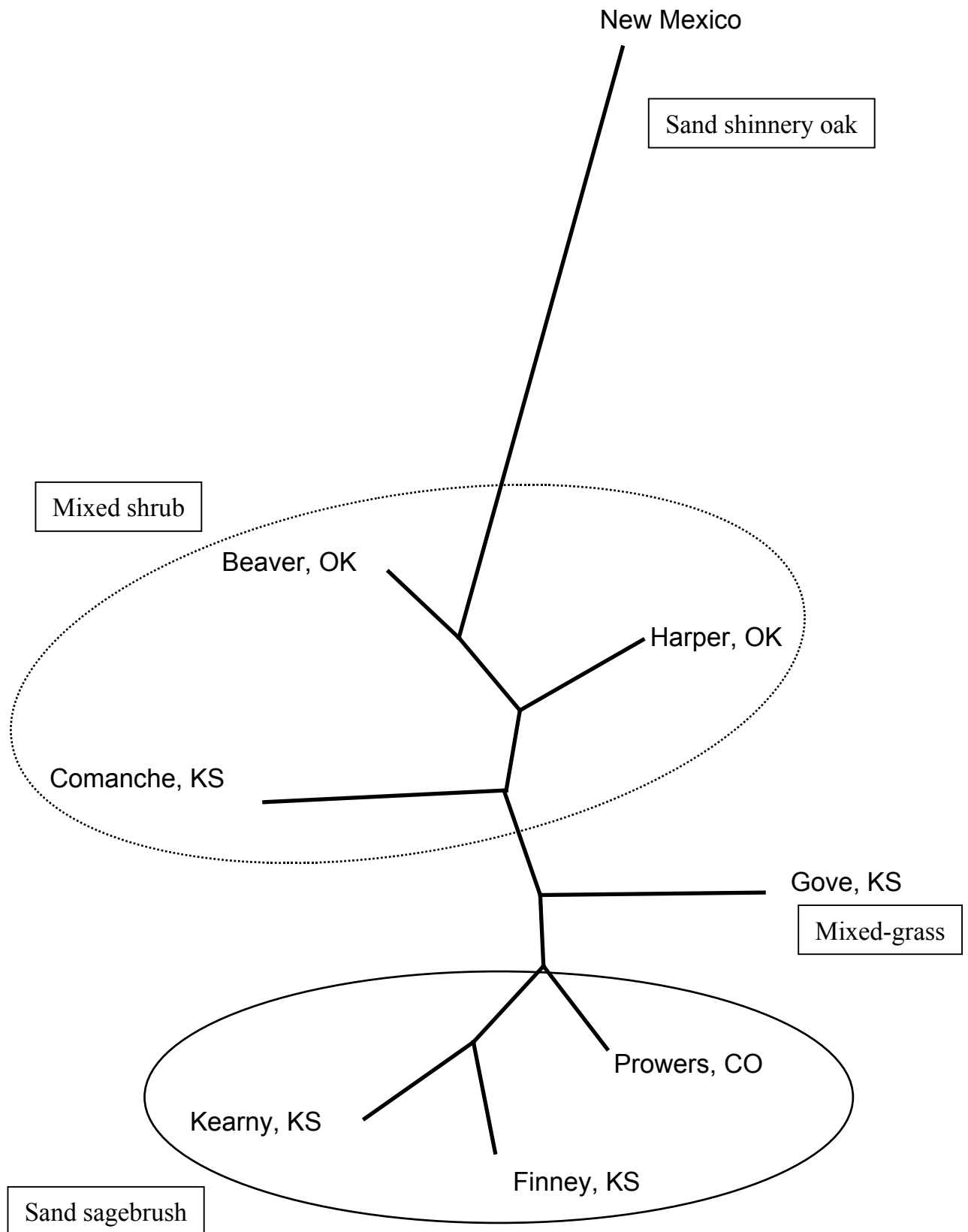


Fig. 2. Frequency of 45 haplotypes (pie charts) by geographic region and sampling sites. Shaded areas depicts current range of lesser prairie-chickens.

Fig. 3. Neighbor-joining tree based on Nei's unbiased minimum distance, habitat specific populations denoted by ellipses and labeled in rectangular boxes. Note the relationship to the geographic structuring of populations reflected in Fig. 2.



APPENDIX II

TABLES OF LESSER PRAIRIE-CHICKEN MORPHOMETRICS

Appendix 2A. Morphometrics ($\bar{x} \pm \text{SD}$) of yearling and adult male and female lesser prairie-chickens Finney County, Kansas 1998–2002.

Measurement ^a	<i>n</i>	Age			Pooled
		Yearling ^b	<i>n</i>	Adult	
Wing-chord(mm)					
Female	3	201.3 ± 4.2	10	202.9 ± 5.4	202.5 ± 4.9
Male	10	205.4 ± 3.9	19	209.6 ± 3.6	208.2 ± 4.1
Tarsus (mm)					
Female	3	49.0 ± 1.4	10	47.4 ± 3.7	47.8 ± 3.4
Male	10	47.7 ± 2.2	20	49.4 ± 2.2	48.8 ± 2.3
Foot (mm)					
Female	3	52.7 ± 2.5	10	51.8 ± 1.6	52.0 ± 1.9
Male	10	54.1 ± 1.9	15	54.3 ± 2.7	54.2 ± 2.4
Mass (g) ^b					
Female	95	709.8 ± 45.3	108	748.9 ± 46.8	730.6 ± 50.3
Male	210	790.1 ± 41.6	294	806.7 ± 40.5	800.2 ± 41.0
Male (Kearny)	3	785.0 ± 27.8	25	796.7 ± 39.0	795.4 ± 29.8

^a The body mass of captured birds was determined to the nearest 5 g on with a Pesola spring scale. Calipers were used to measure tarsometatarsus (tarsus) length and an aluminum wing-chord ruler was used to measure foot length and wing length to the nearest 1 mm. Greatest length of the tarsus was measured from the posterior proximal to the posterior distal. Foot length was measured from back of bent heel to end of middle toe excluding the toenail. Wing length was measured from distal end of the carpal joint to tip of the longest primary, wing pressed flat against ruler.

^b Birds captured in March and April, yearlings \leq 10 months and adults \geq 22 months.

^c Only body mass was measured on males from Kearny County.

Appendix 2B. Morphometrics ($\bar{x} \pm \text{SD}$) of male lesser prairie-chickens captured in Comanche County, Kansas and Prowers County, Colorado 2002.

Measurement ^a	<i>n</i>	Age			Pooled
		Yearling	<i>n</i>	Adult	
Wing-chord(mm)					
Comanche	3	209.4 ± 3.6	9	208.8 ± 2.6	208.7 ± 3.0
Prowers	5	208.0 ± 1.4	9	208.9 ± 4.7	208.6 ± 4.1
Tarsus (mm)					
Comanche	3	54.2 ± 1.2	9	53.3 ± 1.7	53.5 ± 1.6
Prowers	5	54.3 ± 1.3	9	53.6 ± 1.3	53.8 ± 1.3
Foot (mm)					
Comanche	3	48.4 ± 0.6	9	48.3 ± 1.3	48.3 ± 1.0
Prowers	5	49.0 ± 1.0	9	47.5 ± 2.3	47.9 ± 2.1
Mass (g) ^b					
Comanche	3	729.0 ± 57.3	9	751.7 ± 39.2	740.0 ± 48.0
Prowers	5	736.7 ± 12.5	9	764.4 ± 36.8	757.5 ± 34.6

^a The body mass of captured birds was determined to the nearest 5 g on with a Pesola spring scale. Calipers were used to measure tarsometatarsus (tarsus) length and an aluminum wing-chord ruler was used to measure foot length and wing length to the nearest 1 mm. Greatest length of the tarsus was measured from the posterior proximal to the posterior distal. Foot length was measured from back of bent heel to end of middle toe excluding the toenail. Wing length was measured from distal end of the carpal joint to tip of the longest primary, wing pressed flat against ruler.

^b Birds captured in March and April, yearlings \leq 10 months and adults \geq 22 months.

^c Note capture periods for these birds were later in the breeding season than Finney County birds, 24 Apr in Comanche and 30 Apr to 1 May for Prowers. This may explain the lower observed masses as compared to Finney County males (800.2 \pm 41.0 g).